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Population Ecology and Expansion Dynamics of Black-Tailed Prairie Dogs in Western North Dakota

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POPULATION ECOLOGY AND EXPANSION DYNAMICS OF BLACK-TAILED PRAIRIE DOGS IN WESTERN NORTH DAKOTA

by

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ABSTRACT

Black-tailed prairie dogs (Cynomys ludivicianus) are a keystone species that were once widespread throughout the Great Plains. Beginning in the 1900s however, black-tailed prairie dogs experienced serious reductions in range an numbers such that recent estimates suggest they inhabit only 2% of their historic range. As a result of the decline in numbers and range, black-tailed prairie dogs are currently a candidate species for protection under the endangered species act. Because of the species' status as a candidate species and their importance as a keystone species, conservation biologists and resource managers are interested in developing effective management approaches directed towards the conservation and restoration of black-tailed prairie dogs throughout their range.

This thesis is comprised of four chapters that examine various aspects of the population ecology and expansion dynamics of black-tailed prairie dogs in western North Dakota. Chapter one reviews the life history of black-tailed prairie dogs, and discusses current issues regarding the conservation and management of the species. Chapter two describes an experimental study designed to assess the effects of habitat manipulations on the foraging behavior, habitat use, and colony-level expansion of prairie dogs. In Chapter three, a habitat suitability index model for black-tailed prairie dogs was developed to provide biologists and resource managers with sound information to help focus conservation efforts in areas that will most likely support healthy populations of prairie

dogs. Finally, Chapter four estimates both prairie dog density and abundance to help determine the status of prairie dogs in western North Dakota.

To evaluate how habitat manipulation influences colony boundary dynamics, I used a combination of prescribed burns and mechanical brush removal to assess how changes in habitat quality may influence prairie dog behavior, habitat use and colony-level expansion compared to control plots with no habitat manipulations. After two years of conducting behavioral observations and monitoring colony boundary expansion into the treatment plots I found that prairie dogs disproportionately foraged, burrowed, and expanded into experimental treatment plots compared to control plots.

I developed various habitat suitability index model to identify suitable and potential prairie dog habitat in the Little Missouri National Grasslands and at Theodore Roosevelt National Park. Several environmental variables were evaluated as potentially contributing to habitat quality for prairie dogs. Model validation indicated that a positive species habitat- relationship was found between high quality habitat and habitat preference for prairie dogs and that all models performed well in identifying areas of potential prairie dog habitat.

I used visual counts methods to assess prairie dog density and abundance in the Medora and McKenzie Ranger Districts of the Little Missouri National Grasslands and in the South Unit of Theodore Roosevelt National Park. Considerable variation was present in prairie dog density within the Little Missouri National Grasslands and Theodore Roosevelt National Park, however estimated prairie dog densities were within the range of colony densities for black-tailed prairie dogs in the region.

CHA. TER 1

INTRODUCTION

"As we descended from this dome we arrive at a spot, on the gradual descent of the hill, nearly four acres in extent, and covered with small holes. These are the residence of a little animal called by the French petit chien (little dog), which sit erect near the mouth and make a whistling noise, but when alarmed take refuge in their holes. In order to bring them out we poured into one of the holes five barrels of water without filling it, but we dislodged and caught the owner.... We also discovered two frogs in the hole, and near it we killed a dark rattlesnake, which had swallowed a small prairie dog; we were also informed, though never witnessed the fact, that a sort of lizard and snake live habitually with these animals"

--- Lewis and Clark, 1804

Black-tailed prairie dogs (*Cynomys ludovicianus*) are native to short and mixed grass prairies of the United States occupying 11 states, and extending into the plains and plateaus of Canada and Mexico. Historically, black-tailed prairie dogs were widespread throughout their range; however, during the 1900s the species experienced a serious reduction in range and number such that recent estimates suggest they inhabit only 2% of their historic range (Plumb et al. 2001). Factors contributing to this decline include conversion of habitat for agriculture or urban development, habitat modification and fragmentation, introduced disease (sylvatic plague, *Yersinia pestis*; Barnes 1993), and poisoning associated with livestock grazing.

In North Dakota, the historic range of prairie dogs extended across the southwestern portion of the state west of the Missouri River, inhabiting an estimated

3 to 20% of available habitat (Knowles 2001). In the late 1800s and early 1900s prairie dogs were substantially reduced in number to benefit early settlers and the livestock industry. The U.S. Bureau of Biological Survey and the North Dakota Department of Agriculture initiated a poisoning campaign in 1915 (Bell 1921), which affected an estimated 209,429 ha of prairie dog colonies between 1915 and 1964 (Forrest 2002). In 1961 the Bureau of Sport Fisheries and Wildlife reported an estimated 7,990 ha of prairie dog colony in North Dakota (Van Pelt 1999). During this same time period, Bishop and Culbertson (1976) used photographs and other records to document an approximate 89% reduction in the number of prairie dog colonies in one area of southwestern North Dakota between 1938 and 1972. During the period between 1972 and 1978, poisoning on federal lands was more closely regulated and the use of Compound1080, a popular and effective poison for prairie dogs, was prohibited (Reading 1989). Related to changes in management on public lands and the ban of Compound 1080, the decline in prairie dogs was halted and as of the late 1980s an estimated 8,092 ha of prairie dog colonies existed in North Dakota (Van Pelt 1999).

The most recent effort to inventory black-tailed prairie dogs in North Dakota was undertaken by Knowles in 2002. Knowles (2003) reported a minimum estimate of 8,121 ha of prairie dog colonies occurring between two population centers: 1) the Little Missouri Complex, located in western North Dakota primarily along the Little Missouri River, a few tributaries of the Yellowstone River and the upper drainage basins of the Knife and Cannonball Rivers, including the Little Missouri National Grasslands (LMNG) and Theodore Roosevelt National Park (TRNP), and 2) the Standing Rock Complex, located in south-central North Dakota in Sioux County on the Standing Rock Reservation and on adjacent lands in Grant and Morton counties (Knowles and Hagen 2003). Based on Knowles' report (2002), black-tailed prairie dogs occupied 0.16% of their historical distribution within North Dakota in 2002.

Although black-tailed prairie dogs have been drastically reduced in number and range, their grazing and burrowing activities continue to have pronounced effects on ecological processes and biological diversity of prairie ecosystems (Whicker and Detling 1988). For these reasons, the prairie dog is considered a keystone species whose activities have a disproportionate effect on the composition, integrity, and function of prairie communities (Kotliar et al. 1999). The foraging behavior of prairie dogs decreases vegetation height and cover, thereby altering plant species composition and creating open habitats (Coppock et al. 1983, Cincotta et al. 1989). In combination with burrowing activities, prairie dog foraging and grazing can alter the rates of nitrogen uptake by plants (Holland and Detling 1990), and increase nutrient availability to larger herbivores such as bison (*Bos bison*), pronghorn (*Antilocapra americana*) and elk (*Cervus elaphus*) (Wydeven and Dahlgren 1982). Belowground activities of prairie dogs facilitate soil mixing and affect rates of energy and material flows (Ingham and Detling 1984). At the landscape level, variation in colony density and duration of occupancy can lead to a shifting mosaic of patches that vary in vegetation structure, composition, and overall habitat quality, which contribute to increased landscape heterogeneity (Bonham and Lerwick 1976, Archer et al. 1987). Landscape heterogeneity created by prairie dogs can alter the impact of larger disturbances such as fire and other natural disturbances on prairie ecosystem dynamics. For example, the colonies of prairie dog may serve as natural firebreaks and magnify the effects of cyclical and seasonal drought (Coppock and

Detling 1986, Weltzin et al. 1997). By their collective above and below ground activities, prairie dogs attract multiple vertebrate and invertebrate species to colony areas (Knopf and Samson 1997), and it can therefore be argued that by working to conserve black-tailed prairie dogs, we simultaneously maintain key components of prairie ecosystems important for many grassland-dependent plants and animals. Specific examples of species that are obligatorily associated with prairie dogs or prairie dog colonies include the federally endangered black-footed ferret (*Mustela nigripes*) and mountain plover (*Charadrius montanus*), swift fox (*Vulpes velox*), burrowing owls (*Athene cunicularia*) and numerous other amphibians and reptiles (Miller et al. 1994).

Prairie Dog Ecology

Taxonomic and Morphological Description

The black-tailed prairie dog is a ground squirrel belonging to the Sciuridae family. Taxonomists currently recognize five living species of prairie dogs: white-tailed prairie dogs (*Cynomys leucurus*), Utah prairie dogs (*C. parvidens*), Gunnison's prairie dogs (*C. gunnisoni*), Mexican prairie dogs (*C. mexicanus*), and black-tailed prairie dogs (Holliser 1916, MacClintock 1970, Clark et al. 1971, Pizzimenti 1975, Hall 1981). All five species of prairie dog are within the genus *Cynomys*, which is divided into two subgenera: *Leucocrossuromys* (includes the white-tailed, Gunnison's, and Utah prairie dog species) and *Cynomys* (includes the Mexican and black-tailed prairie dogs) (Hollister 1916, Pizzimenti 1975). White-tailed, Utah, and Gunnison's prairie dogs have short tails (30-65 mm), hibernate for several months a year, and live in mid-high-grass meadows at elevations of 1,700-3,000 m. Mexican and black-tailed prairie dogs have relatively longer tails (60-110 mm) with a distinctive black tip, do not hibernate, and live in short to mixed-grass prairies at altitudes of 700-1,700 m. Of the five species of prairie dogs the black-tailed prairie dog is the most common, and the focal species for this research project.

Prairie Dog Diet

Black-tailed prairie dogs are herbivores that feed on a variety of grasses, herbaceous vegetation, and occasionally insects (Hoogland 1995). Diets of prairie dogs can be highly variable related to spatial and temporal variation in plant phenology and plant communities within the range of the species (Fagerstone 1979, Clippinger 1989). Grass and sedge species are important in the diet of prairie dogs year round (Tileston and Lechleitner 1966, Summers and Linder 1978, Ursek 1984), whereas forbs and seeds become more important in fall and winter (Koford 1958, Bohan and Lerwick 1976, Ursek 1984). Western wheatgrass (*Agropyron smithii*), blue grama (*Bouteloua gracilis*), and buffalo grass (*Buchloe dactyloides*) are among the most common grasses consumed by prairie dogs (Bohan and Lerwick 1976, Fagerstone 1979, Koford 1958, Ursek 1984,). However, sand dropseed (*Sporobolus cryptandrus*), threadleaf sedge (*Carex filifolia*), sixweeks fescue (*Vulpia octoflora*), and downy brome (*Bromus tectorum*) can often be important components of the diets of prairie dogs (Hansen and Gold 1977, Ursek 1984). Forbs commonly consumed by prairie dogs include fringed sagewort (*Artemisia frigida*), scarlet globe mallow (*Sphaeralcea coccinea*), rabbit brush (*Chrysothamnus nauseosus*), Russian thistle (*Salsola kali*), saltbush (*Atriplex sp.*), fetid marigold (*Dyssodia popposa)*, and plains prickly pear (*Opuntia polyacantha*) (King 1955, Koford 1958, Summers and Linder 1978, Garret et al. 1982, Wydeven and Dahlgren 1982). Although prairie dogs avoid eating threeawn (*Atistida oligantha*), horseweed (*Conyza canadensis*), buffalo bur

(*Solanum rostratum*), and prairie dogweed (*Dyssodia papposa*), they will often clip down these species to increase visibility (King 1955, Tileston and Lechleitner 1966). Finally, Koford (1958) noted that prairie dogs avoid consuming and clipping plains milkweed (*Asclepias pumila*), snow on the mountain (*Euphorbia marginata*), and bee plant (*Cleome serrulata*).

Habitat

Prairie dogs have long been known to occur in areas where there is low to sparse vegetation (Merriam 1902), related to a preference for habitats with relatively low vegetation cover of 7-13 cm (Koford 1958, Clark et al. 1982, Agnew et al. 1986). Low vegetative cover enhances visibility and the ability of prairie dogs to detect predators (Hoogland 1995). Prairie dogs typically avoid foraging in tree stands and areas heavily dominated by shrubs with relatively tall, thick vegetation (Hoogland 1995). Although not a preferred habitat, prairie dogs will expand into areas of sagebrush and other tall vegetation by clipping and uprooting these plants at the periphery of existing colonies (Osborn 1942). Similarly, the colonies of prairie dogs may also expand into areas that have been heavily grazed or disturbed (Reid 1954). Via their foraging and clipping behavior, prairie dogs actively alter vegetation structure and maintain plants within colonies in an early growth state, thereby decreasing vegetative height, increasing bare ground and increasing percent forb cover (Koford 1958). Plant communities within prairie dog colonies are different from adjacent plant communities, typically including a variety of grasses and forbs such as western wheatgrass, blue grama, buffalo grass, sixweeks fescue, tumble grass (*Panicum spp.*), hairy grama (*Bouteloua hirsuta*), hairy triodia grass, sand dropseed, scarlet globe mallow, plains prickly pear, Russian thistle, fringed sagwort, and fetid marigold (Koford 1958, Knowles 1982, Wydeven and Dahlgren 1982,Clippinger 1989).

Prairie dogs are semifossorial rodents considered to require soils capable of supporting complex burrow systems without flooding or collapsing (Koford 1958). Therefore, prairie dogs tend to avoid fine sandy soils and instead establish colonies in areas with deep, well-drained Elloam soils that retain water and promote burrow stability. In the Great Plains prairie dog colonies are typically found on fine to medium textured alluvial soils (Reid 1954, Koford 1958, Knowles 1986). In the state of North Dakota, prairie dog colonies have been found on clay loam soils located on river benches and upland plateaus (Reid 1954). Although it is well known that prairie dogs prefer loamy soils, expansion dynamics associated with high density populations may cause prairie dogs to burrow into less favorable surrounding areas such as clay or soft lignite (Koford 1958). Because burrows occur in many soil types, soil association may not directly limit prairie dog distribution. Rather the indirect effects that textures have on soil moisture and vegetation may be more important in determining prairie dog presence (Koford 1958).

Prairie dog colonies have been observed across a wide range of slopes throughout their distributional range. In general, however, prairie dogs avoid extremely flat or low-lying areas subject to seasonal flooding, and areas with high-density vegetation that hinders predator detection (Koford 1958). In North Dakota, prairie dogs avoid slopes greater than 25% (Reid 1954). In South Dakota, biologists have suggested that prairie dogs prefer slopes ranging from 2 to 5% and are limited by slopes ranging from 9 to 45% (Koford 1958, Sheets 1970, Dalsted 1981). In other states, researchers have suggested an optimal slope of 0 to 15% (Koford 1958, Tileston and Lechleitner 1966, Knowles 1986, Clippinger 1989, Reading and Matchett 1997). In northern portions of their range prairie dogs may prefer south facing slopes because higher solar exposure promotes warmth during winter and rapid vegetation growth during the spring and summer (Koford 1958).

Population Demographics

Black-tailed prairie dogs are diurnal social burrowing rodents that live in colonies consisting of a matrix of burrows and underground tunnels (Hoogland 1995). Within these colonies are reproductive units known as coteries, which typically contain one adult male, one to six adult females and juvenile and subadult offspring (Hoogland 1981). Coterie territory areas typically range in size from 0.5 ha to 1.01 ha (Hoogland 1995). Coterie territories are vigorously defended such that the activities and home ranges of coterie members are restricted to coterie boundaries. Larger coteries may contain two breeding adult males, or an adult male may control two smaller adjacent coteries. Within coteries prairie dogs interact cooperatively with other coterie members, by assisting in raising young, scanning for, announcing and mobbing predators, allogrooming, and defending territory areas (Hoogland 1995).

The mating system of the black-tailed prairie dog is described as a type of female or harem defense polygyny in which the variance in reproductive success is higher for males than for females (Hoogland and Foltz 1982). Male and female prairie dogs reach sexual maturity at two years of age, but some females may breed as yearlings when food resources are abundant and competition is low (Hoogland 1995 and King 1955). Females are monestrus, with the annual mating season limited to a two to three week period beginning in late February-early April (Anthony and Foreman 1951, King 1955, Tileston and Lechleitner 1966). After a 34-35 day gestation period an average of four (range = one to eight) blind and hairless pups are born (Anthony and Forman 1951). In late May-early June pups are weaned and emerge from their natal burrows. Shortly thereafter, male-biased natal dispersal begins as young of the year vacate natal coteries and attempt to establish positions in other coteries within the local colony or in nearby colonies (Cully 1997). Female black-tailed prairie dogs usually remain in their natal coterie throughout their lives, whereas males disperse out of their natal coteries as juveniles or yearlings. Similar to other species, male-biased dispersal in black-tailed prairie dogs is a mechanism for inbreeding avoidance that promotes genetic diversity within and among prairie dog colonies (Hoogland 1982, Garret and Franklin 1983).

Inter and intracolony dispersal movements occur as a response to the availability of food and mating opportunities (Garret and Franklin 1988) and ultimately drive colony expansion. Garret et al. (1982) reported that the expansion of black-tailed prairie dogs occurs primarily when suitable habitat is available in areas surrounding the colony. In the absence of suitable habitat, prairie dogs will forage on or crop taller grasses and vegetation around the colony margin, thereby stimulating the growth of shorter graminoid forage plants and facilitating colony expansion. Intensive foraging by prairie dogs on these preferred graminoids eventually promotes less desired herbaceous forbs (Archer et al. 1987). Because of these effects, vegetation zones in roughly concentric rings are often produced on prairie dog colonies (Bonham and Lerwick 1976). Vegetation in the center or core regions of prairie dog colonies is dominated by low growing forbs where a complex of multiple well-developed burrows are used for sleeping and reproductive activities. These "dome-mound" or "crater" burrows are typically large in diameter (1 to

3 m) with significant mounding (height = 0.3-1 m) and bare soil around the burrow entrance (Cincotta 1989, Hoogland 1995). Adjacent to colony core areas are graminoid-dominated grasslands, which serve as primary foraging areas for colony members. Within these graminoid-dominated areas multiple, relatively shallow "satellite" burrows are excavated and used during exploratory movements and to provide protective cover while foraging. The outermost edges of colonies are the zones of colony expansion where newly clipped grasslands or shrublands have not yet converted to lower growing graminoid-dominated grasslands. Over time prairie dog colonies expand and shift over the landscape as intensive foraging in graminoid-dominated areas depletes forage, forbs become more prevalent, and edge areas are enlarged into previously unoccupied habitats. As the colony enlarges and expands into adjacent prair[illegible]unded burrows in the interior regions of colonies are gradually abandoned as foraging areas become more distant and satellite burrows are converted into deeper dome-mound burrows (Hoogland 1995). Behavioral studies have demonstrated that some portion of the territories of nearly all coteries within a prairie dog colony extends into graminoid-dominated foraging areas. Further, prairie dogs that reside in coteries without access to graminoid grasslands experience lower survivoral and reproduction rates (Garrett and Franklin 1988).

The level of colony expansion and the presence of suitable prairie dog habitat is dependent on several natural and anthropogenic variables. Changes in colony boundaries not initiated by poisoning or shooting can generally be attributed to changes in vegetative cover (Kotford 1958, Franklin and Garrett 1988). Based on Norland and Bradybaugh's (unpublished report) review of prairie dog colony fluctuations at Theodore Roosevelt National Park, climate and grazing-related changes in vegetation cover influenced temporal changes in colony area and size. Other factors influencing vegetative cover include herbicide control, fire, and other human-induced disturbances. Colony fluctuations due to precipitation and changes in grazing pressure can be examined in Figure 2.3 (Chapter 2). The most noticeable change in total colony acreage was between 1953 and 1956 when a reduction in grazing pressure associated with the removal of domestic livestock from the park, temporarily low densities of native ungulates, and above-normal precipitation may have combined to promote increased vegetative cover. Estimated acreages of prairie dog colonies at Theodore Roosevelt National Park recovered and gradually increased between 1957 to 1973 during a prolonged period of below average precipitation. There was apparently a lull in colony area expansion by prairie dogs around 1973 due to above average precipitation. After the mid 1970s prairie dog colony acreage at Theodore Roosevelt National Park has been increasing related to normal or below-normal precipitation and increased grazing pressure by expanding populations of native ungulates including reintroduced elk (*Cervus elaphus*).

Behavior

Prairie dogs exhibit a suite of individual behaviors that maintain and strengthen coterie bonds and increase colony fitness including amicable interactions among coterie members, territorial disputes, and predator alarm calls. Within coteries, members often engage in amicable interactions such as allogrooming, mouth-to-mouth interactions or "kisses". However, when pregnant or lactating, females may become hostile while defending their nursery burrows (Hoogland 1995). Territorial disputes between coterie members involves staring, tooth chattering, flaring of the tail, bluff charges, and occasional physical combat. Upon detection of threatening predators, prairie dogs will warn others in and around their coteries using a repetitious anti-predator call. This initial warning call often triggers a chain reaction of warning calls by other prairie dogs in the colony. Other routine behaviors exhibited by prairie dogs include the territorial "jump-yip" display, mound building, collecting nest material, foraging and clipping vegetation, and basking in the sun.

Prairie Ecosystem Dynamics

Historically, the Great Plains supported relatively high density, mobile populations of large-bodied mammalian herbivores (Hartnett et al. 1996). Large grazing herbivores remove significant amounts of standing and accumulated aboveground biomass, and in association with other nongrazing activities, bison in particular had a pronounced effect on prairie ecosystems (Frank and Groffam 1998, Green 1998, Knapp et al. 1999). In general, grazing herbivores modify vegetation in numerous ways including: (1) reducing plant height, (2) altering plant morphology, (3) increasing nitrogen levels in aboveground plant tissues, (4) creating a mosaic of patchiness in otherwise ungrazed landscapes, (5) altering the proportion of biomass among various plant functional groups including live/dead biomass ratios, (6) altering rates of energy and material flow through below ground consumers, and (7) altering plant species diversity and species richness by selective grazing/browsing (Damhoureyeh and Hartnett 1997, Augustine and McNaughton 1998, Collins et al. 1998, Frank and Groffman 1998). Notwithstanding the influence of climate on plant productivity, fire strongly influences ungulate grazing patterns by altering forage plant selectivity at the fine scale and driving habitat selection at the larger local and landscape levels (Coppedge et al. 1998).

In general, periodic fire and grazing by terrestrial herbivores are the two most important factors influencing community and ecosystem dynamics in prairie grasslands (Weltzin et al. 1997, Collins et al. 1998). Fire is an important natural disturbance process in prairie ecosystems, which functions to enhance species diversity and productivity of prairie grasslands, and appears necessary to prevent invasion and establishment of woody species (Coppedge et al. 1998). Combined experimental and descriptive research indicates that periodic fire (wildfire or controlled burns) results in a series of changes in prairie ecosystems that alter terrestrial nutrient cycling, maintain high levels of plant species diversity, and introduce significant spatial heterogeneity in prairie grasslands (Knapp et al. 1998, Ajwa et al. 1999, Valone and Kelt 1999). The most obvious and immediate effect of fire is the removal of accumulated standing and senescent plant material, which exposes soils to higher levels of sunlight resulting in greater solar input and warmer soil temperatures. These conditions alter multiple soil and litter processes (decomposition, microbial-mediated mineralization of organic nitrogen to inorganic nitrogen, denitrification, etc.), promote the growth of C_4 grasses, and eventually lead to important changes in plant carbon allocations and nitrogen use efficiency (Blair et al. 1998). Accelerated growth of nitrogen rich plants in burned areas attracts large, grazing ungulates (Biondini et al. 1999), which, while consuming significant amounts of plant tissue, also return much of the ingested plant nitrogen to the soil surface in the form of dung and urine (Frank et al. 1994).

The tendency for grazers to selectively forage on the pulse of new growth following a fire may significantly improve habitat conditions for prairie dogs, thereby facilitating expansion of prairie dog colonies by increased foraging opportunities and dispersal. Although not yet observed by rigorous study, anecdotal evidence supports the hypothesis that grazing pressure and periodic fire influence prairie dog colony dynamics. The pronounced decline in prairie dogs in North America after the late 1800s was coincident with the removal of vast herds of bison and the effective suppression of wildfire. It may be possible to restore habitat and populations of prairie dogs in the Great Plains region by reintroducing fire into prairie ecosystems, ultimately benefiting the many species associated with prairie dogs in grassland ecosystems (Miller et al. 1994).

Current Management and Status of Black-Tailed Prairie Dogs

In July 1998, the National Wildlife Federation and the Biodiversity Legal Foundation petitioned the U.S. Fish and Wildlife Service (USFWS), to emergency list the black-tailed prairie dog as a threatened species under the Endangered Species Act (ESA). In response, the USFWS initiated a nine-month review of the status of prairie dogs across their range. In 2000, the USFWS ruled that the petition to list the black-tailed prairie dog was warranted but precluded because of higher priority species (FWS 2000). Currently, the USFWS conducts annual reviews of the status of black-tailed prairie dogs to determine if any significant changes have occurred that may warrant higher priority listing.

Although not federally protected under the ESA, a Conservation Agreement was developed by various state, federal, tribal and private entities. The Conservation Agreement embraces two main components: 1) a Conservation Assessment, which describes the current status of the black-tailed prairie dog and identifies threats to prairie dog populations, and 2) a Conservation Strategy, which focuses on reducing or eliminating threats to the viability of prairie dogs (Van Pelt 1999). The interstate conservation team developed a Multi-state Conservation Plan for the Black-tailed Prairie Dog in the U.S., which determined acreage goals for each state based on potential habitat, and suggested a 15% increase in overall acreage in ten years (Luce 2003). Additional targets of the conservation plan include: 1) maintaining two complexes greater than 2,023 hectares in the U.S., 2) create and maintain at least nine new complexes greater than 2,023 hectares, 3) manage greater than 10% of total occupied habitat in complexes greater than 405 hectares, and 4) maintain distribution over more than 75% of the counties in the historical range (Luce 2003). Of the 11 states within the historic range of prairie dogs, eight have signed the multi-state management plan. Under the interstate black-tailed prairie dog proposal, North Dakota would have been required to increase prairie dog acreage from 8, 092 ha to 44,506 hectares of prairie dog colonies

In response to the petition to list black-tailed prairie dogs under the ESA and the Mulit-state Conservation Plan, the North Dakota Game and Fish Department along with the North Dakota Prairie Dog Advisory Group, met and developed a state specific management plan with the goal of maintaining a biologically viable population of black-tailed prairie dogs in North Dakota. Based on the recent population trends for black-tailed prairie dogs in North Dakota as inferred from data on estimated colony acreages and a population viability assessment completed by Knowles (2001), North Dakota's approximate 8,092 hectares of prairie dog colonies were considered to represent a viable population. Important in this viability assessment was the assumption that sylvatic plague will not become a significant population-limiting factor for prairie dogs in the state (Knowles 2001).

Related to the statewide viability assessment and an opinion by the North Dakota Prairie Dog Advisory Group, the North Dakota Game and Fish Department did not support or join with the other regional states in the Multi-state Conservation Plan for the Black-tailed Prairie Dog (NDGF 2001). Nevertheless, North Dakota expressed a commitment to maintain a viable population of black-tailed prairie dogs in North Dakota by monitoring prairie dog populations and their status. As part of this commitment, the distribution of colonies of black-tailed prairie dogs within their range in North Dakota was recently mapped (Knowles 2003), and this study is working to estimate prairie dog density and abundance within the Little Missouri National Grasslands. In addition, several research projects are being conducted to provide sound information for the future management of black-tailed prairie dogs in North Dakota.

Objectives of Study

Because of the growing concern over the status of prairie dogs and their associated species, it has become increasingly important to know and understand the population dynamics of the black-tailed prairie dog. Therefore, the foundation of this research project is to provide insight into the population dynamics of prairie dogs and provide management tools to promote viable prairie dog populations and their associated species while decreasing conflict with humans.

At Theodore Roosevelt National Park (Figure 1.1), black-tailed prairie dogs are expanding and thereby coming into conflict with visitor use facilities (picnic grounds, campgrounds), raising public health concerns related to the potential for disease transmission of sylvatic plague by infected fleas from prairie dogs to humans. As a direct result of prairie dog expansion, the Peaceful Valley Picnic Area was recently closed and relocated (Theodore Roosevelt National Park Environmental Assessment, April 2001). Related to expanding prairie dogs at Theodore Roosevelt National Park, resource managers are interested in how the implementation of a new fire management program (minimal control of natural wildfires and periodic controlled burns) will influence prairie dogs and whether controlled burns may be useful in influencing the distribution and movements of prairie dogs at the landscape level. In response to the desire to naturally control expanding prairie dogs at Theodore Roosevelt National Park, an experimental study was designed to assess the effects of fire on the foraging behavior, habitat use, and colony-level expansion of prairie dogs. Knowledge of how prairie dogs respond to fire is important because most remaining large populations of this threatened species are located in national parks and national grasslands, which are beginning to or are otherwise interested in implementing active fire management programs to reestablish natural disturbance regimes and thereby restore vascular plant communities to some semblance of pre-European conditions.

In an effort to help manage and recover black-tailed prairie dogs in western North Dakota (Figure 1), a Habitat Suitability Index (HSI) model was constructed using various environmental variables to predict areas of suitable habitat. Habitat Suitability Models are simplifications of real world systems that provide a framework around which qualitative and quantitative habitat relationships can be structured into testable hypotheses for wildlife management decision-making (Schamberger and O'Neil 1986). Because increased emphasis has been placed on scientific based decision-making, HSI models can become important tools for managing wildlife. As a complement to the above research objectives (assessing how fire affects prairie dog ecology) a HSI model will provide biologists with sound information to help focus conservation efforts in areas that are most likely to support healthy prairie dog colonies and their associated species.

As part of the Dakota Prairie Grasslands revised management plan, resource management objectives for the Little Missouri National Grassland (Figure 1.1) provides for maintaining plant and animal diversity and assuring long-term viable populations and recovery of sensitive species and their habitats. In accordance with this plan and the Black-tailed Prairie Dog State Management Plan, the United States Forest Service (USFS) is monitoring and managing for viable populations of black-tailed prairie dogs and the possible future reintroduction of the black-footed ferret. In this study, monitoring techniques for estimating prairie dog densities were adapted from a field methodology employed by Severson and Plumb (1998). Visual counts were preformed on several pre-selected colonies within the Little Missouri National Grasslands and Theodore Roosevelt National Park as a direct form of assessing prairie dog populations. Data from this research will provide the USFS with information regarding prairie dog abundance/density within the Little Missouri National Grasslands and Theodore Roosevelt National Park (Figure 1), as well as the opportunity to compare densities of prairie dogs to total colony area from colony maps that were completed in 2002. This information is important for biologists to assess the current status of black-tailed prairie dogs, and to identify population trends in western North Dakota for the future management of the species.

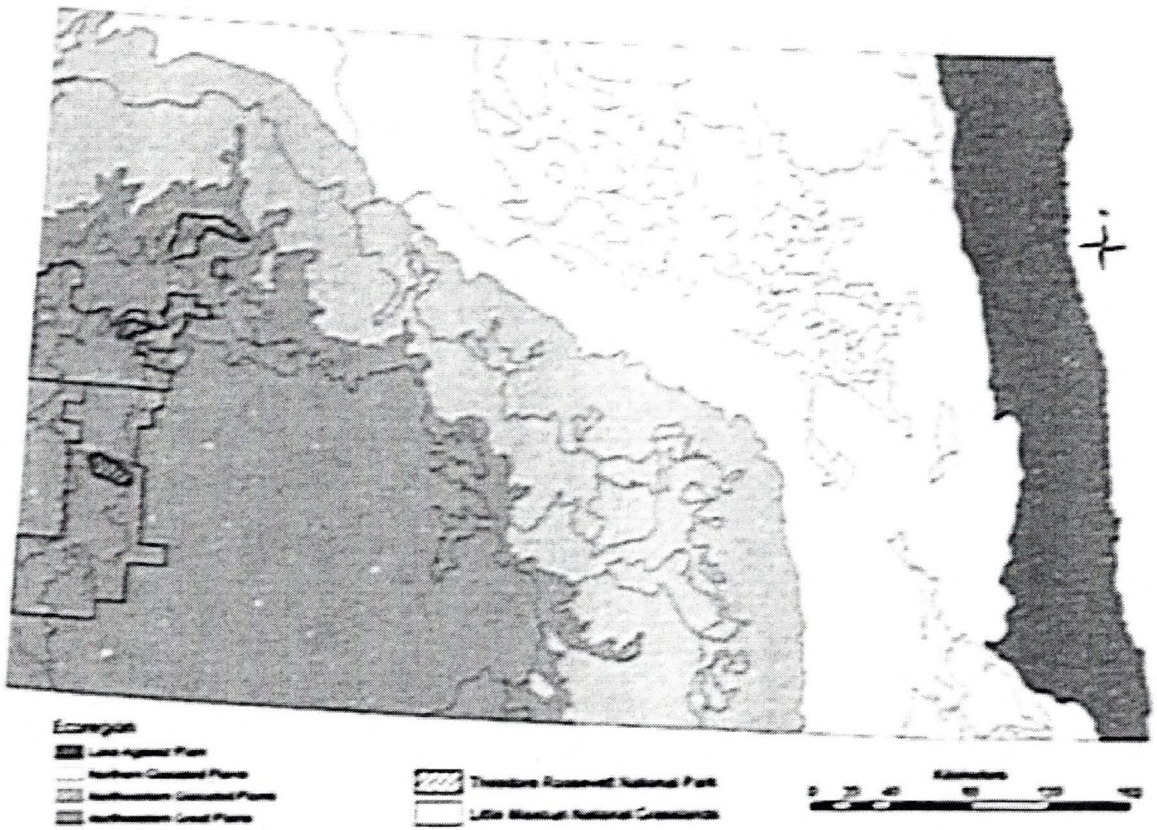


Figure 1. The Little Missouri National Grasslands and Theodore Roosevelt National Park in relation to the ecoregions of North Dakota

CHAPTER 2

EXPERIMENTAL EVALUATION OF EXPANSION DYNAMICS OF BLACK-TAILED PRAIRIE DOGS AT THEODORE ROOSEVELT NATIONAL PARK

"Around the prairie-dog towns it is always well to keep a look-out for the smaller carnivora, especially coyotes and badgers...and for the larger kinds of hawks. Rattlesnakes are quite plenty, living in the deserted holes, and the latter are also the homes of the little burrowing owls."

---Theodore Roosevelt

Introduction

Black-tailed prairie dogs (*Cynomys ludovicianus*) are native to short and mixed grass prairies of the United States, occupying parts of 11 states, and extending into the plains and plateaus of Canada and Mexico. Historically, black-tailed prairie dogs were widespread throughout their range; however, during the 1900s black-tailed prairie dogs experienced serious reductions in range and numbers such that recent estimates suggest they inhabit only 2% of their historic range (Plumb et al. 2001). Factors contributing to this decline include conversion of habitat for agriculture or urban development, habitat modification and fragmentation, introduced disease (sylvatic plague, *Yersinia pestis*; Barnes 1993), and poisoning associated with livestock grazing (Plumb et al. 2001).

Although black-tailed prairie dogs have been drastically reduced in number and range, the foraging and burrowing activities of the species continue to promote significant natural heterogeneity in prairie grasslands where they remain abundant. Their collective above and belowground activities create mosaics of habitat across the landscape, which attract multiple vertebrate and invertebrate species to colony areas (Knopf and Samson 1997). For these reasons, the prairie dog is considered a keystone species whose activities have a disproportionate effect on the composition, integrity, and function of prairie communities (Kotliar et al. 1999). Specific examples of species that are associated with prairie dogs or prairie dog colonies include the federally endangered black-footed ferret (*Mustela nigripes*) and mountain plover (*Charadrius montanus*), swift fox (*Vulpes velox*), burrowing owls (*Athene cunicularia*) and numerous amphibians and reptiles (Koliar et al. 1999). Therefore it can be argued that by working to conserve black-tailed prairie dogs, we simultaneously maintain key components of prairie ecosystems important for multiple grassland dependent plants and animals (Miller et al. 1994).

Black-tailed prairie dogs are social burrowing rodents that live in colonies consisting of a matrix of burrows and underground tunnels (Hoogland 1995). Within these colonies are harem defense based polygynous reproductive units known as coteries, which typically contain one adult male, one to six adult females and juvenile and subadult offspring (Hoogland 1981). Coterie territorial areas typically range in size from 0.5 ha to 1.01 ha (Hoogland 1995), and are vigorously defended such that the activities and home ranges of coterie members are restricted to coterie boundaries. Male and female prairie dogs reach sexual maturity at two years of age, but some females may breed as yearlings when food resources are abundant and competition is low (King 1955, Hoogland 1995). Females are monestrus, with the annual mating season limited to a two to three week period beginning in late February- early April (Anthony and Foreman 1951, King 1955, Tileston and Lechleitner 1966). After a 34-35 day gestation period, an average of four (ranging from one to eight) blind and hairless pups are born (Anthony and Forman 1951). In late May-early June pups are weaned and emerge from their natal burrows. Shortly thereafter, male-biased natal dispersal begins as young of the year vacate natal coteries and attempt to establish positions in other coteries within the local colony or in nearby colonies (Cully 1997). Female prairie dogs usually remain in their natal coterie throughout their lives. Similar to other species, male-biased dispersal in black-tailed prairie dogs is a mechanism for inbreeding avoidance that promotes genetic diversity within and among prairie dog colonies (Hoogland 1982, Garret and Franklin 1988). Inter and intracolony dispersal movements by individual animals occur as a response to the availability of food and mating opportunities (Garret and Franklin 1988), and ultimately drive colony expansion.

Garret et al. (1982) reported that the expansion of black-tailed prairie dogs occurred primarily when suitable habitat was available in areas surrounding colonies. Suitable habitat may be considered to include areas with relatively low growing plants and low densities of trees and woody shrubs where foraging and burrowing prairie dogs are better able to detect approaching predators. This suggestion is supported by the observation that prairie dogs actively maintain a buffer of clipped vegetation around colony peripheries, and then gradually expand into buffer areas as buffer areas are extended (Hoogland 1982). In general, observations of natural changes in the boundaries of colonies of black-tailed prairie dogs have consistently been attributed to relatively low vegetation in the areas of expansion (Reid 1954, Kotford 1958, Uresk et al. 1981, Franklin and Garrett 1983).

Fire and fire in combination with grazing by terrestrial herbivores are major drivers of community and ecosystem dynamics in prairie grasslands (Frank et al. 1994, Weltzin et al. 1997, Collins et al. 1998, Biondini et al. 1999). Combined experimental and descriptive research indicates that periodic fire (wildfire or controlled burns) results in a series of changes in prairie ecosystems that alter terrestrial nutrient cycling, maintain high levels of plant species diversity, and introduce significant spatial heterogeneity in prairie grasslands (Blair et al. 1998, Knapp et al. 1998, Ajwa et al. 1999, Valone and Kelt 1999). However, the most obvious and immediate effect of fire that is of importance for prairie dogs may be the suppression or removal of woody shrubs and accumulated plant biomass (Coppedge et al. 1998). If reduced herbaceous cover and more nutritious plant growth associated with fire improves foraging and dispersal opportunities for prairie dogs, expansion of prairie dog colonies may be non-randomly oriented toward recent burns when they occur near or adjacent to existing colonies. It is also possible that mechanical brush removal may enhance habitat quality for prairie dogs by improving conditions for detecting predators.

Although black-tailed prairie dogs are declining in many areas, at Theodore Roosevelt National Park the species has been increasing and several colonies have recently encroached on visitor use facilities (picnic grounds, campgrounds). Because lethal control is not a feasible option for managing wildlife in national parks in general, biologists at Theodore Roosevelt National Park are interested in developing "natural" mechanisms for managing expanding prairie dog colonies. Moreover a new fire management program was recently approved that includes provisions for minimal control of natural wildfires and periodic controlled burns to restore degraded habitats. Because any fire near a colony will likely improve habitat suitability for prairie dogs, it may be important to consider the potential effects of periodic wildfires and controlled burns on colony expansion. Finally, if mechanical brush removal enhances habitat quality for prairie dogs in similar ways as fire, active habitat management may prove useful for directing colony expansion when controlled burning is not otherwise feasible.

Because of their importance as a "keystone species" and "ecosystem engineers," conservation biologists and resource managers alike are interested in developing effective management approaches for black-tailed prairie dogs. I designed an experimental study to assess how habitat manipulations (controlled burns, mechanical brush removals) would influence black-tailed prairie dogs. The research was conducted at Theodore Roosevelt National Park where I selected three prairie dog colonies for replicate study (Figure 2). As further detailed below, I used a combination of prescribed burns and mechanical brush removals to test the prediction that prairie dogs would disproportionately forage, burrow and expand into experimental treatment plots compared to adjacent control plots. My combination of detailed behavioral observations, periodic burrow surveys, and mapping of colony boundaries revealed a strong positive response by prairie dogs to these types of habitat manipulations. The implications of the study include that it might be possible to appropriately manage and facilitate the restoration of black-tailed prairie dogs by carefully applied habitat manipulations, ultimately benefiting the multiple species associated with prairie dogs in North American grassland ecosystems.

Study Area

Theodore Roosevelt National Park is located long the Little Missouri River corridor within the badlands of western North Dakota. The park contains more than

28,000 ha divided among the South Unit, the North Unit and the Elkhorn Ranch Unit. All study colonies were located in the South Unit of the park on the Little Missouri Plateau, which is characterized by flat plateaus, rugged canyons, and alluvial benches produced by the Little Missouri River and it tributaries (Figure 3). Soils within the park belong to the Bainville Series; a soil type derived from excessively drained medium-texture, calcareous parent material. Dominant vegetation includes western wheatgrass (*Agropyron smithii*), blue grama (*Bouteloua gracilis*), little bluestem (*Andropyron scoparius*) and silver sagebrush (*Artemisia cana*) on the prairies and rolling hills, rocky mountain juniper (*Juniperus scopularum*) and green ash (*Fraxinus pennsylvanica*) along the woody draws, and eastern cottonwood (*Populus deltoides*) along the river. The climate is characterized as arid with long cold winters and short hot summers. Temperatures range from an average low of −11.6 °C in January to an average high of 22 °C in July. Average annual rainfall is 381 mm, with most precipitation falling in early summer (May-June).

History of Prairie Dogs at Theodore Roosevelt National Park

Prairie dog colonies at Theodore Roosevelt National Park have a recent history of expansion with periods of fluctuation in total colony acreage mainly attributed to drought and grazing pressure (Norland and Bradybaugh unpublished report; Figure 4). Between 1947 and 1953, livestock grazing was common within the park and grazing pressure by livestock maintained relatively low vegetation, thereby providing prairie dogs the opportunity to expand from 83 ha in 1947 to 345 ha in 1953. A sharp decline in colony acreage after 1953 resulted from illegal poisoning of several prairie dog colonies, such that colony acreage was reduced to an estimated 95 ha in 1956. Cattle were

Figure 2. Maps illustrating the layout of the experimental treatment and control plots at each of the three prairie dog colonies selected for research. Black lines are the measured boundary for each prairie dog colony at the start of the study (May 2002) before burn and mechanical brush removal treatments in the experimental plots. Experimental plots at the (a) Peaceful Valley, (b) Mike Auney, and (c) Johnson's Plateau study colonies had 2.2, 1.7, and 1.7 hectares of area for potential colony expansion as of May 4, 2002, control plots had 1.8, 2.1, and 2.0 hectares of area for potential colony expansion.

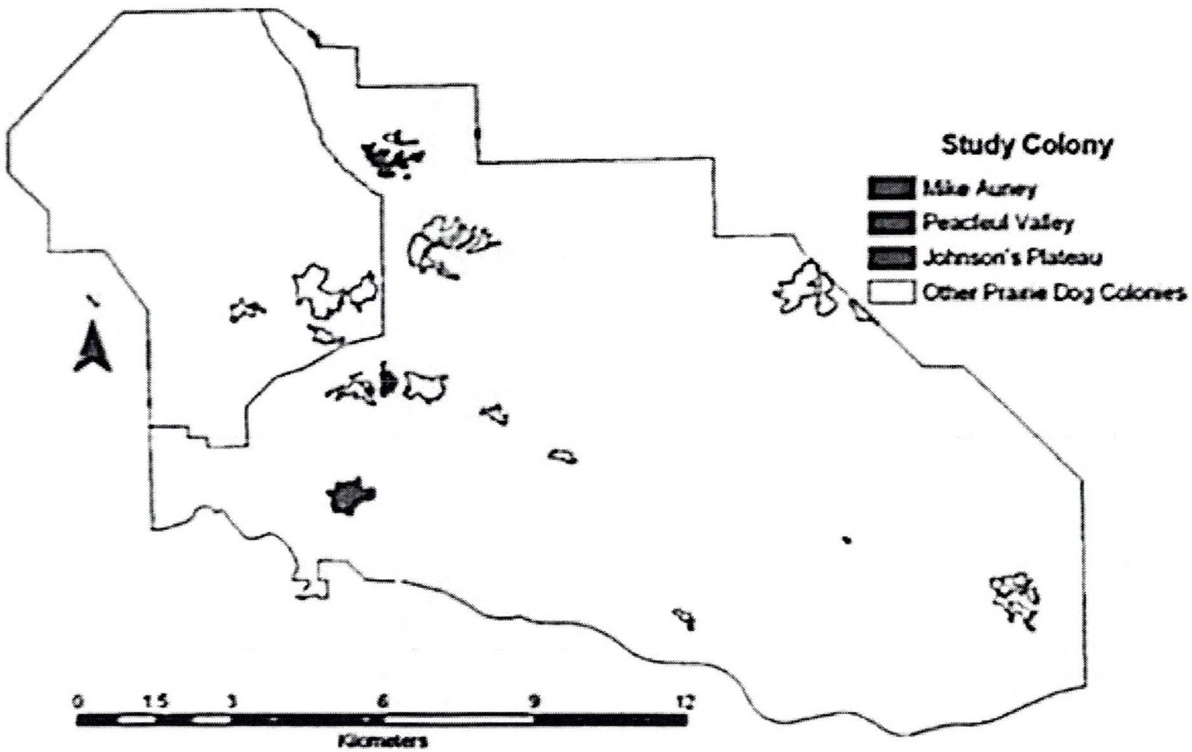


Figure 3. Map illustrating the locations of the three prairie dog study colonies in relation to other prairie dog colonies in the South Unit of Theodore Roosevelt National Park in 2003.

removed from the park in 1954, and as vegetation recovered from intensive grazing, several periods of above-average rainfall may have prevented colony expansion by the pulse of vegetation growth, resulting in the lowest acreage recorded at the park in 1957. After 1957, grazing by bison (*Bos Bison*) and feral horses (*Equus caballus*) in combination with below average rainfall were thought to have contributed to an expansion to an estimated 165 ha by 1963. Colony acreage remained stable between 1963 and 1979. Over the past 25 years prairie dog colony acreage has gradually and continually increased, potentially due to increased grazing pressure as native ungulates increased and elk (*Cervus elaphus*) were reintroduced. Currently, the Theodore Roosevelt National Park area encompasses all or most of 23 active prairie dog colonies, occupying an estimated 439 ha in the South Unit, and 59 ha in the North Unit.

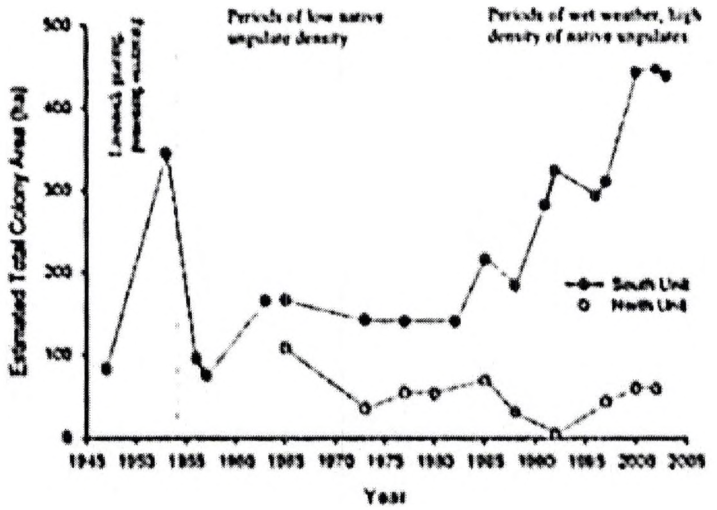


Figure 4. Fluctuations in estimated total colony area at Theodore Roosevelt National Park between 1947 and 2003. Data were attained from TRNP records, Norland and Bradybaugh (no date), and Knowles (2002).

Methods

Preliminary surveys in fall 2001 identified 3-4 study colonies for experimental study. Research was subsequently conducted over two field seasons in summer 2002 and summer 2003. In summer 2002 research was initiated in early April and completed in late September. In summer 2003 research was initiated in early April and completed in late August 2003. In fall 2001, three prairie dog colonies, Johnson's Plateau, Mike Auney, and Peaceful Valley were selected from the South Unit of the park, each with a recent history of expansion and vegetation and topographical features that would allow prairie dogs the opportunity to continue to expand. An experimental study was designed, whereby randomly chosen 200 m x100 m (two ha) experimental plots were delineated at the edge of each study colony and burned with a corresponding two-hectare control plot left unburned (Figure 2). Two-hectare treatment and control plots were delineated to assure that each treatment would abut two or more coteries, thereby minimizing the potential effects of inter-colony differences in dispersal and movements independent of burn experiments. Burns were originally scheduled for early spring 2002 to coincide with the dispersal of yearling males in spring-early summer (Garrett and Franklin 1988, Hoogland 1995). This burn schedule would have allowed dispersing individuals the opportunity to move into burned areas. Due to inclement weather, however, burns were not completed until late May 2002, after substantial green-up had occurred. The late application of burn treatments resulted in patchy and incomplete burns at all three study colonies. To compensate for the lack of removal of all sage and other herbaceous vegetation, all remaining vegetation was mechanically removed from the experimental plots approximately one month following prescribed burns in late June 2002.

Immediately following the burn treatments, I initiated a program of systematic observations of prairie dog foraging and habitat use associated with all treatment and control plots. Scan-sampling methods (Altmann 1974) were used to collect observational data on prairie dog social interactions (amicable and aggressive) foraging, vigilance, running, resting, and burrowing activities. All observations were conducted with a Leica Apo Televid 20x- 60x spotting scope mounted to a four-meter observation tower equipped with a blind. The observation stand was positioned near the experimental treatment and control plots where both plots were readily visible. A rotating schedule of observations was used to collect similar numbers of hours of behavioral data for each study colony each week from mid-May to September in 2002 and from mid-May to August in 2003. In 2002, 12 hrs /colony /week were recorded, divided among five time periods: 0600 to 0900 hrs, 0900 to 1100 hrs, 1200 to 1500 hrs, 1500 to1800 hrs, and 1800 to 2100 hrs. Because prairie dogs exhibited a significant amount of expansion into the experimental plots relative to the control plots in 2002, the number of hours of behavioral observations was reduced to include only the periods of highest prairie dog activity: 0600 to 1100 hrs and 1800 to 2100 hrs (Severson and Plumb 1998) in summer 2003.

Differences in vegetative structure between the treatment and control plots may affect the ability to observe prairie dogs, thereby introducing a bias to data collected on foraging and habitat use in the different plots. I used a procedure developed by Menkens et al. (1990) to assess the visibility of prairie dogs and correct for potential differences in sightability among areas varying in visual obstruction. Visual obstruction was estimated for each colony by randomly placing artificial prairie dogs (25cm X 15cm brown paper bags filled with sand) throughout each treatment and control plot (Menkens et al. 1990).

An observer not involved in the placement of artificial prairie dogs scanned and recorded the number of prairie dogs seen in each treatment plot from an observation tower as if conducting behavioral observations. Visual obstruction was determined by the percentage of artificial prairie dogs missed during each scan. The number of prairie dogs observed during behavioral observations was then corrected using a formula developed by Menkens et al. (1990).

Estimates of changes in area and directionality in colony expansion in the treatment and control plots at each study colony were used to assess whether fire/mechanical removal of vegetation influenced landscape-level distribution of prairie dogs. Digital maps of colony boundaries were constructed using a Trimble ASCI GPS unit based on methods described by Plumb et al. (2001). Colony boundaries were mapped by walking along the colony peripheries, where the colony periphery was defined to include all active burrows within five meters of clipped vegetation. As an additional measure of colony expansion, data were collected on all new burrows excavated by prairie dogs in the different plots. New burrows were defined to include all of the burrows that were excavated in either the experimental or control plots after burn treatments were applied in late May 2002. All active and non-active burrows were counted, with all non-active burrows identified by burying a steel nail into the ground around the rim of each burrow. Active and inactive burrows were later relocated with a metal detector. Any newly active burrows or new satellite burrows were continually identified by the absence of a nail marker and burrows that were inactive or became inactive were also marked. Active burrows were defined as burrows with fresh fecal pellets, tracks, freshly dug dirt around the rim of the mound, lack of vegetation on the mound, and those with observations of prairie dogs entering or exiting. Every month throughout the duration of the field season (April-September), maps of colony boundaries and burrow counts were updated to quantify changes in burrows and burrowing activities related to prairie dog dispersal movements and colony-level expansion or retraction. Additionally, in 2003, a Trimble ASCI GPS unit with sub-meter accuracy was used to collect spatial and attribute data on all active and non-active burrows encountered in the study plots. Each burrow was given a permanent identification number with corresponding UTM coordinates, and relocated monthly to reassess burrow status as active or inactive.

Vegetation may limit the ability of prairie dogs to detect predators; therefore I assessed aspects of vegetative structure in the treatment plots for all study colonies in 2002 and 2003. Each experimental treatment and control plot was divided into eight 50 m x 50 m quadrants, four along the back of the plot and four along the front of the plot. To ensure a representative sample of each plot, one randomly chosen quadrant was selected from both the front and back of the study plot for vegetation sampling each month in the field seasons of 2002 and 2003. I used a circular plot sampling method to measure multiple aspects of vegetative cover in the plots. Height of grass/herbaceous vegetation was measured at nine points at intervals of five meters along the centerlines of two 20 m transects bisecting the sampling unit. Percent cover was estimated by measuring the widest portion of the shrub canopy for each shrub within the sampling unit. Number of shrubs/woody vegetation within the sampling unit was also recorded.

I assessed prairie dog density on each study colony to evaluate whether prairie dog expansion was linked to this parameter. I used visual count methods adapted from

Severson and Plumb (1998) as a direct means of determining population density. To ensure an unbiased assessment of prairie dog populations, two observers conducted counts for three consecutive days from mid-June to mid-August when the rate of population change in prairie dog colonies is considered to be the lowest. Visual counts were conducted once in July 2002, and once a month from June to August in 2003. To ensure a representative sample of each colony, minimums of two study plots, ranging in size from two to four hectares (depending on colony size), were established on each study colony. Observers entered a four-meter observation tower equipped with a blind at least 30 minutes prior to the first count each morning. Five consecutive counts at 20-minute intervals were conducted each morning between 0700 and 1100 hrs. During each count observers systematically scanned each plot using 10 x 50 mm binoculars and recorded the maximum number of prairie dogs seen. Severson and Plumb (1998) found that visual counts using the maximum sample count rather than the mean number of animals counted yielded a positive significant relationship with population estimates derived from mark-recapture techniques for the same colonies (Fagerstone and Biggins 1986, Menkens et al. 1990). Therefore, the maximum number of prairie dogs recorded per sampling effort was used to calculate prairie dog density for each study colony. Prior to the first count each morning, weather conditions were recorded using a Kestrel 3000 weather system (Nielsen- Kellerman, Boothwyn, PA). Because strong winds (> 32 km/h) and inclement weather (rain, wind speeds > 32 km/h) can restrict above-ground activity of prairie dogs, counts were limited to periods with no precipitation, wind speed < 32 km/h, and ambient temperatures > 10 °C. Data on prairie dog density were calculated based on the model $P = ([Y/S_p] - 3.04)/0.04$, where Y is the maximum count of prairie dogs in a replicate for each colony and S_p is the total area sampled adjusted for the probability of not observing all prairie dogs during a count.

Data Analysis

Log-linear models were used to evaluate prairie dog foraging, vigilant, and burrowing activities between treatments for both years. When comparing models, I used the Raftery's Bayesian Information Criterion (BIC) to identify the best-fit model. The model with the lowest BIC is assumed to be the most parsimonious model and thus the model that best describes prairie dog behavior between treatments (SYSTAT 8.0, 1998). Because of multiple habitat manipulations occurring at different times in 2002, data on the area of new expansion were analyzed separately by month using one-way analysis of variance (Zar 1999). I also used a one-way ANOVA to compare the total number of burrows present in each treatment plot prior to the experiment to the number of total burrows in each treatment plot at the end of 2002. This type of analysis was performed to account for any effect the total number of burrows present prior to the experiment may have had on the rate of increase of new burrows in either the experimental treatment or control plots. No habitat manipulations occurred in 2003, however, and a repeated measures ANOVA was used to assess differences in the area of new expansion and total number of burrows between the experimental treatment and control plots. Vegetation data were analyzed separately by month using two-sample *t*-tests (Zar 1999) in 2002, and repeated measures ANOVA in 2003. Data on percent shrub cover were not normally distributed; data were therefore transformed by the arcsin method to meet test assumptions. All means are presented ± 1 SE and statistical analyses were completed using SYSTAT 8.0 statistical software package (SPSS Inc., Chicago, IL).

Results

Habitat Manipulation

The combined burn and mechanical brush removal treatments is the experimental plots in May and June of 2002 reduced shrub cover and herbaceous plant height in the experimental treatment plots relative to the control plots (Figures 5 a,b, 6 a,b, 7 a,b; Table 1, 2). Prior to the experiment, the experimental plots had an average percent shrub cover of 21.20 ± 8.01% and an average herbaceous height of 23.83 ± 8.01cm; two years after habitat manipulation, the experimental plots had an average percent cover of 0.56 ± 0.30% and an average herbaceous height of 11.50 ± 4.84 cm. Percent cover and average herbaceous height in the control plots remained relatively constant from the beginning to the end of the experiment (April 2002: 20.40 ± 7.61% shrub cover and 26.17 ± 4.76 cm average herbaceous height; Aug 2003: 20.96 ± 9.97% shrub cover and 25.83 ± 1.08 cm average herbaceous height).

Response to Burn and Brush Removal Treatments

Prairie dogs responded to the experimental treatments in 2002 by a disproportionate expansion into the treatment plots at all three study colonies by the end of that summer ($F_{1,4}$ = 14.241, P = 0.001; Figure 5 c, 6 c, 7 c). Notably, I observed almost no expansion into the treatment areas of the three study colonies in the month after the incomplete burn (0.06 ± 0.04 ha). In contrast, in the three months after burn and brush removal treatments, prairie dogs had expanded an average of 1.05 ± 0.39 ha into the experimental plots compared to an average of 0.00 ± 0.0 ha into the control plots by early September 2002 (July, $F_{1,4}$ = 20.705, , P = 0.010; Aug, $F_{1,4}$ = 10.514, P = 0.032; Sep, $F_{1,4}$ = 9.190, P = 0.039). In summer 2003 there was limited additional expansion by

Table 1. Summary of vegetation and habitat characteristics for experimental treatment and control plots at Mike Auney (MA), Johnson's Plateau (JP), Peaceful Valley (PV) prairie dog colonies at Theodore Roosevelt National Park during the summer of 2002. Data were based on measurements taken monthly during the period from April to August. Means are ± 1 SE.

		Shrub Cover (%)		Mean Herbaceous ht (cm)		Mean Number of Shrubs		Shrub Density (#/m^2)	
Month	Colony	Treatment	Control	Treatment	Control	Treatment	Control	Treatment	Control
April	MA	17.05	14.15	17.67 ± 3.67	32.39 ± 4.15	15.50	25.00	0.05	0.08
	JP	20.17	5.06	35.83 ± 2.88	29.86 ± 2.57	29.50	14.00	0.00	0.01
	PV	26.35	42.00	16.17 ± 4.62	18.22 ± 3.99	36.00	17.00	0.00	0.01
	Mean[1]	21.20 ± 8.01^{a}	20.40 ± 7.61^{a}	23.83 ± 4.04^{a}	26.17 ± 4.76^{a}	27.00 ± 5.87^{a}	18.67 ± 4.68^{a}	0.09 ± 0.02^{a}	0.06 ± 0.01^{a}
May	MA	27.22	25.71	5.33 ± 1.06	19.83 ± 3.04	29.50	17.50	0.09	0.06
	JP	3.93	15.04	9.78 ± 2.66	20.61 ± 2.12	13.00	16.50	0.00	0.01
	PV	2.96	36.87	7.17 ± 1.37	15.33 ± 2.99	23.50	21.00	0.00	0.01
	Mean[1]	11.37 ± 5.23^{a}	25.87 ± 11.23^{a}	7.50 ± 1.43^{a}	18.50 ± 2.58^{b}	22.00 ± 4.60^{a}	18.33 ± 5.91^{a}	0.07 ± 0.01^{a}	0.06 ± 0.02^{a}
June	MA	1.28	15.18	9.11 ± 1.45	27.61 ± 4.34	2.50	6.00	0.01	0.03
	JP	18.70	6.47	11.83 ± 2.69	40.06 ± 3.51	3.00	13.00	0.00	0.01
	PV	1.77	43.57	7.78 ± 1.65	37.11 ± 3.69	2.00	12.00	0.00	0.01
	Mean[1]	1.95 ± 0.81^{a}	21.74 ± 12.06^{a}	9.67 ± 0.99^{a}	34.83 ± 4.48^{b}	2.50 ± 1.15^{a}	11.17 ± 2.68^{b}	0.01 ± 0.00^{a}	0.04 ± 0.01^{b}
August	MA	0.04	64.90	2.78 ± 0.76	23.50 ± 4.83	1.00	10.00	0.00	0.03
	JP	0.00	13.95	9.50 ± 2.35	30.50 ± 4.04	0.00	31.00	0.00	0.01
	PV	0.06	23.33	3.11 ± 0.74	21.83 ± 5.92	1.00	9.00	0.00	0.01
	Mean[1]	0.03 ± 0.02^{a}	34.06 ± 14.72^{b}	5.00 ± 1.71^{a}	25.33 ± 4.02^{b}	0.67 ± 0.42^{a}	14.5 ± 4.30^{b}	0.00 ± 0.00^{a}	0.05 ± 0.01^{b}
September	MA	1.07	15.52	3.50 ± 1.03	10.11 ± 3.91	1.50	7.50	0.00	0.02
	JP	0.53	0.57	6.78 ± 1.99	24.28 ± 2.80	1.00	2.50	0.00	0.01
	PV	0.76	15.27	5.16 ± 2.78	30.22 ± 4.92	4.00	16.50	0.00	0.01
	Mean[1]	0.79 ± 0.27^{a}	10.45 ± 5.75^{a}	5.17 ± 1.19^{a}	21.67 ± 4.98^{b}	2.17 ± 0.65^{a}	8.83 ± 4.00^{a}	0.01 ± 0.00^{a}	0.03 ± 0.01^{a}

[1]Means were compared between treatment and control using t-tests. Superscripts with different letters indicate that means were different at the P <0.05 levels. Significant levels were based on separate variance alphas when the standard deviations for the means differed by at least a factor of two, otherwise pooled variance alphas were used.

Table 2 Summary of vegetation and habitat characteristics for experimental treatment and control plots at Mike Auney (MA), Johnson's Plateau (JP), Peaceful Valley (PV) prairie dog colonies at Theodore Roosevelt National Park during the summer of 2003. Data were based on measurements taken monthly during the period from April to August. Means are ± 1 SE.

		Shrub Cover (%)		Mean Herbaceous ht (cm)		Mean Number of Shrubs		Shrub Density (#/m²)	
Month	Colony	Treatment	Control	Treatment	Control	Treatment	Control	Treatment	Control
April	MA	1.00	24.00	1.44 ± 0.47	7.33 ± 1.57	0.50	17.00	0.00	0.05
	JP	4.96	0.19	7.72 ± 1.94	24.11 ± 2.64	3.50	13.50	0.01	0.04
	PV	0.00	50.33	3.28 ± 0.70	12.28 ± 2.51	0.00	4.50	0.00	0.01
May	MA	16.92	3.54	10.28 ± 1.31	14.72 ± 2.47	2.50	8.00	0.01	0.03
	JP	2.43	0.87	7.28 ± 1.41	23.33 ± 2.86	3.50	5.00	0.01	0.02
	PV	0.25	50.00	5.44 ± 1.20	16.89 ± 3.32	7.50	9.50	0.02	0.03
June	MA	10.58	12.80	14.22 ± 3.02	17.33 ± 2.04	4.00	15.00	0.01	0.05
	JP	13.03	18.16	21.72 ± 3.41	25.72 ± 1.74	10.50	11.00	0.03	0.04
	PV	1.62	50.00	12.94 ± 1.78	20.00 ± 2.79	7.50	8.50	0.02	0.03
July	MA	3.01	13.23	15.78 ± 3.03	17.39 ± 3.02	2.00	8.00	0.01	0.03
	JP	1.05	3.60	10.28 ± 1.89	22.39 ± 2.94	4.50	6.50	0.01	0.02
	PV	0.62	11.63	8.39 ± 1.58	19.89 ± 3.20	1.50	18.50	0.00	0.06
August	MA	0.78	11.43	5.83 ± 1.23	28.44 ± 3.34	1.00	10.00	0.00	0.03
	JP	0.89	13.23	26.61 ± 3.35	25.17 ± 2.88	6.00	16.00	0.02	0.05
	PV	0.01	38.20	4.89 ± 1.39	24.94 ± 4.01	0.50	13.00	0.00	0.04
All Months Mean[1]		3.81 ± 1.52 ^{a}	16.78 ± 4.93 ^{b}	10.07 ± 1.38 ^{a}	20.10 ± 1.46 ^{b}	3.67 ± 0.93 ^{a}	10.93 ± 1.38 ^{b}	0.01 ± 0.00 ^{a}	0.03 ± 0.00 ^{b}

[1] Superscripts with different letters indicate that means were different at the $P<0.01$ levels

prairie dogs into the treatment areas, but the overall expansion at the end of the study in September 2003 remained higher for the treatment plots compared to the controls ($F_{1,4}$ = 8.042, P = 0.047; Table 3, Figure 8, 9, 10).

In accordance with the observation of disproportionate expansion in experimental plots, new burrowing was also greater for experimental compared to control plots (Figure 11). By the end of summer 2002, prairie dogs had excavated an average of 215 ± 52.4 new burrows in the experimental plots compared to an average of 60 ± 13.6 new burrows in the control plots ($F_{1,8}$ = 6.908, P = 0.030; Table 4). By the end of summer 2003, I had noted an average total of 335 ± 77.9 new burrows in the experimental treatment plots compared to an average of 69 ± 23.6 new burrows in the control plots ($F_{1,4}$ = 14.425, P = 0.019; Table 4).

Prairie Dog Behaviors

Related to their anti-predator behaviors I hypothesized that prairie dogs would spend more time in the experimental plots than in the control plots, which would be reflected by observations of more prairie dogs and increased levels of foraging and burrowing in experimental compared to the control plots. I also proposed that prairie dogs venturing into control plots would exhibit more vigilance because of the higher vegetative cover in control compared to burn and brush removal treated plots. After the habitat manipulations in 2002, I observed a higher mean number of prairie dogs in the experimental plots than in the control plots for all months (Jun, $F_{1,4}$ = 15.109, P = 0.018; Jul, $F_{1,4}$ =14.225, P = 0.020; Aug, $F_{1,4}$ = 21.516, P =0.010; Sep, $F_{1,4}$ = 7.647, P = 0.051; Figure 12 a). When I adjusted for apparent differences in sightability (on average the chance of missing a prairie dog in the experimental treatment and control plots was 4 ±

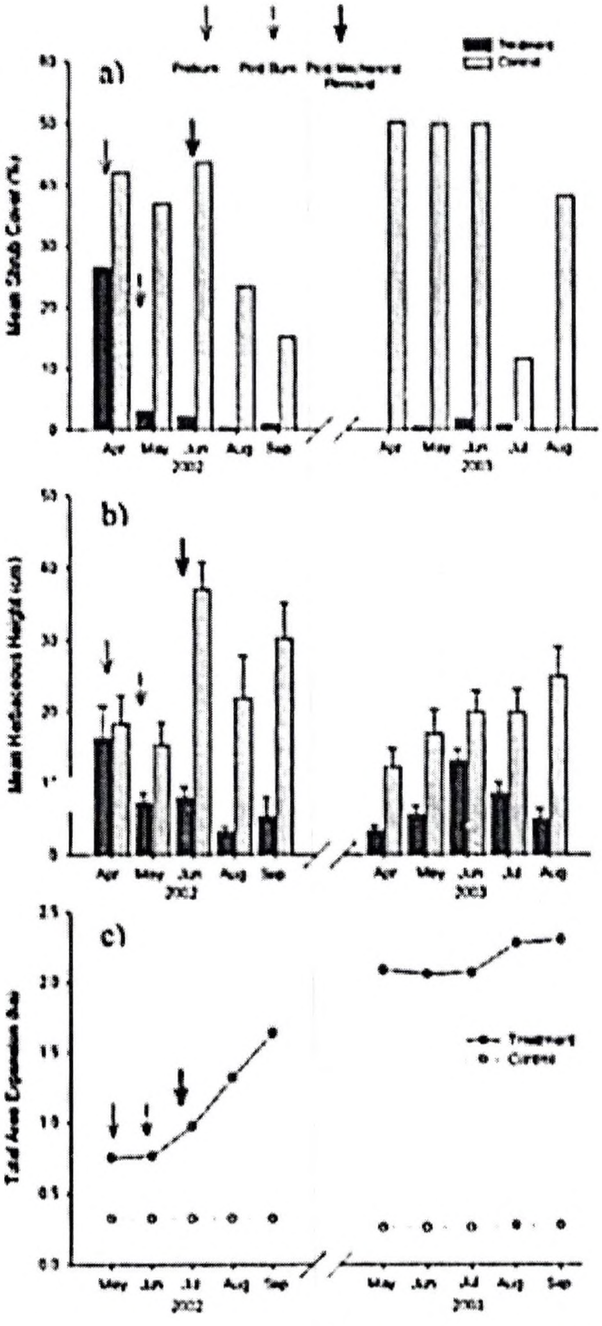


Figure 5. Variation in (a) shrub cover, (b) herbaceous plant height, and (c) colony expansion in the experimental treatment and control plots for Peaceful Valley study colony during the summer of 2002 and 2003. Percent shrub cover and herbaceous height were based on measurements from randomly placed circular plots each month of each field season. Colony boundaries were mapped monthly using a global positioning unit. See methods for additional details. Bars are1 ± SE.

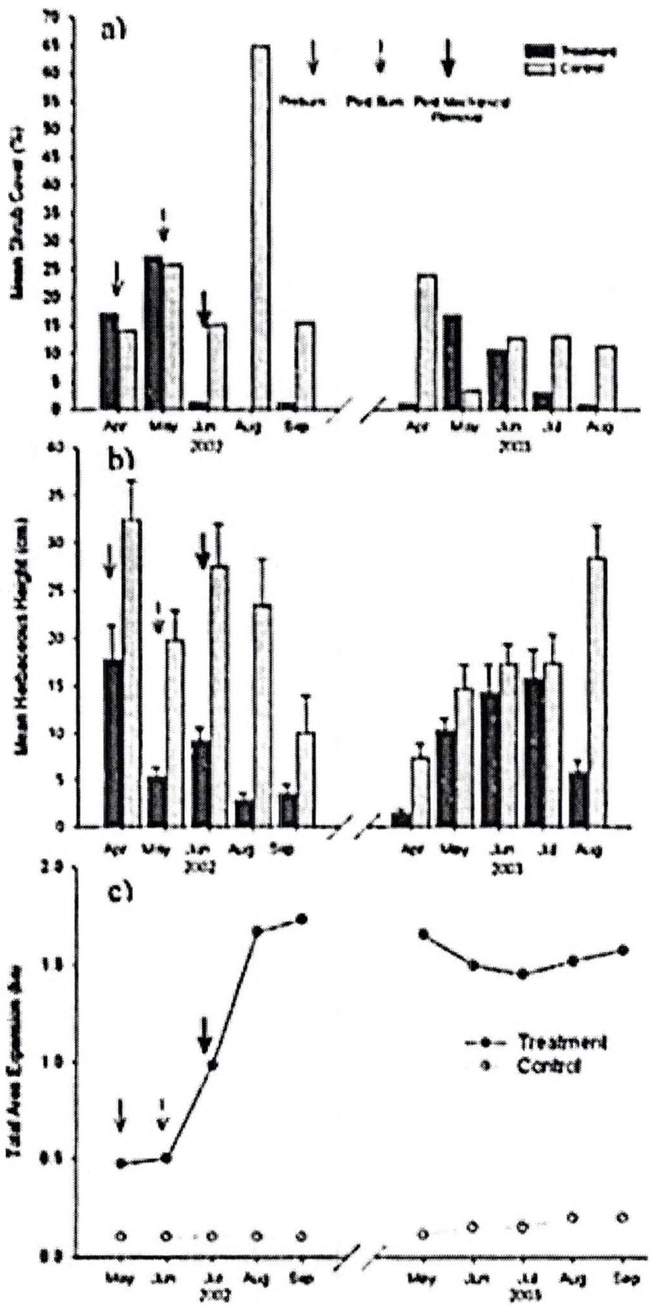


Figure 6. Variation in (a) shrub cover, (b) herbaceous plant height, and (c) colony expansion in the experimental treatment and control plots for Mike Auney study colony during the summer of 2002 and 2003. Percent shrub cover and herbaceous height were based on measurements from randomly placed circular plots each month of each field season. Colony boundaries were mapped monthly using a global positioning unit. See methods for additional details. Bars are 1 ± SE.

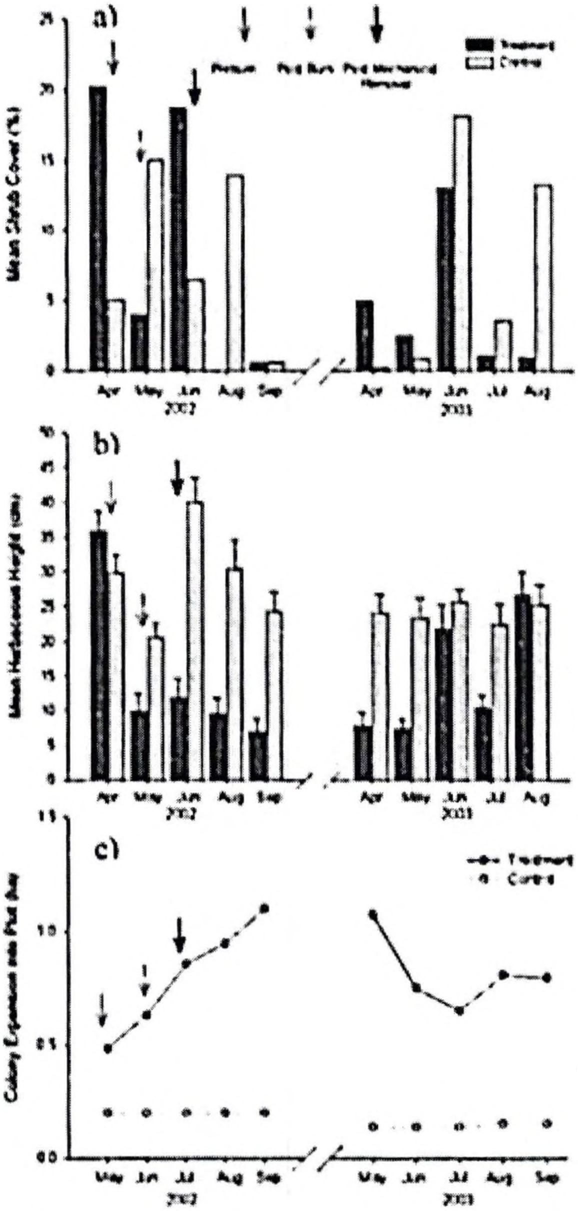


Figure 7. Variation in (a) shrub cover, (b) herbaceous plant height, and (c) colony expansion in the experimental treatment and control plots for Johnson's Plateau study colony during the summer of 2002 and 2003. Percent shrub cover and herbaceous height were based on measurements from randomly placed circular plots each month of each field season. Colony boundaries were mapped monthly using a global positioning unit. See methods for additional details. Bars are ±1 SE.

Table 3. Estimated area of expansion (ha) of prairie dog colonies at three study colonies at Theodore Roosevelt National Park during the summers of 2002 and 2003. Means are ± 1 SE.

	2002[1]		2003[2]	
Prairie dog colony	Treatment	Control	Treatment	Control
Peaceful Valley	0.885 (40%)[3]	0	1.557 (70%)	-0.047
Mike Auney	1.255 (74%)	0	1.092 (63%)	0.095 (5%)
Johnson's Plateau	0.616 (36%)	0	0.312 (18%)	-0.045
Mean	0.919 ± 0.19	0 ± 0.00	0.987 ± 0.36	0.001 ± 0.047

[1] Area of new expansion after burn treatment in 2002.
[2]Total area of expansion including expansion in 2002 and any new expansion in 2003.
[3]Percent of total area available in plot as of May 2002 that was colonized.

Table 4. Estimated number of new burrows in treatment and control plots at three study colonies at Theodore Roosevelt National Park during the summers of 2002 and 2003. Means are ± 1 SE.

	2002[1]		2003[2]	
Prairie dog colony	Treatment	Control	Treatment	Control
Peaceful Valley	192	40	458	41
Mike Auney	315	86	358	116
Johnson's Plateau	138	54	191	50
Mean	215 ± 52.4	60 ± 13.6	335 ± 77.9	69 ± 23.6

[1]Number of burrows includes all new excavated burrows in 2002.
[2]Number of burrows includes new burrows excavated in 2002 and new burrows excavated in 2003.

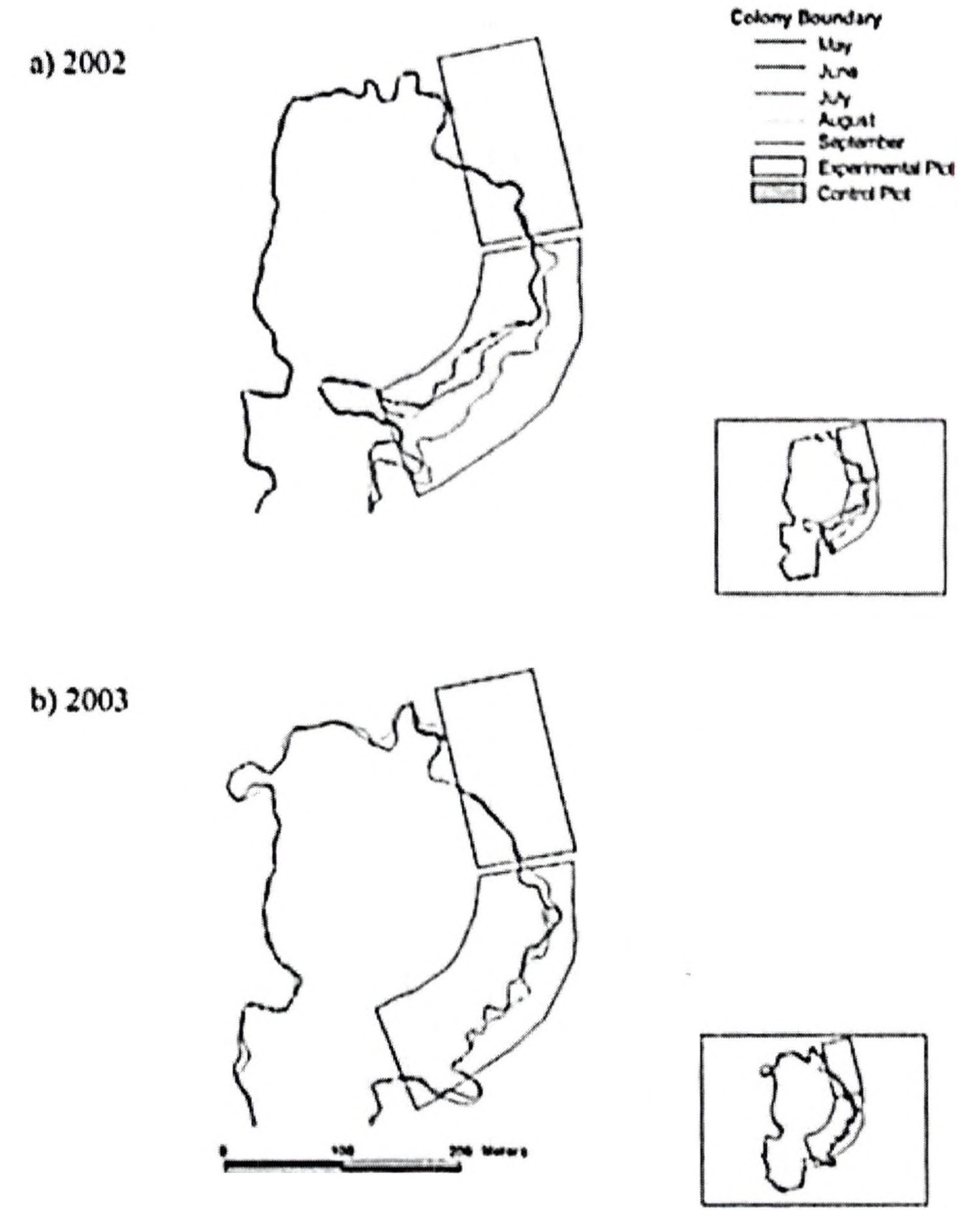
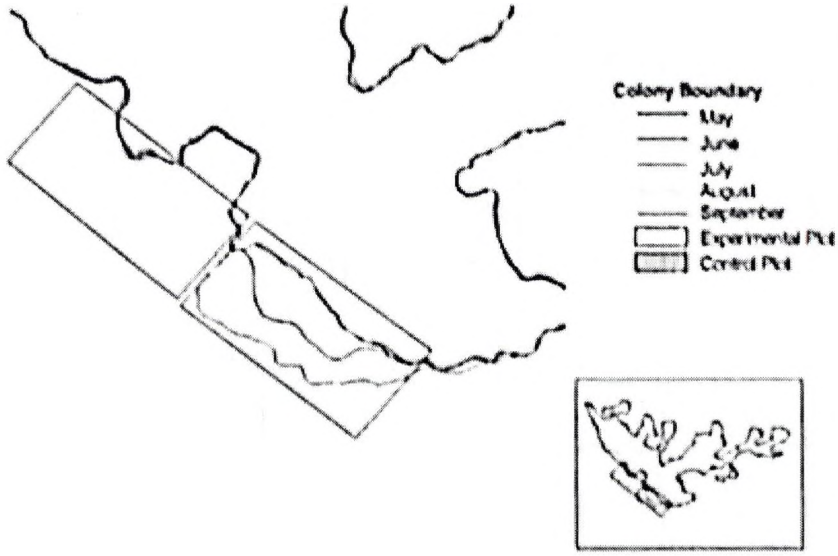


Figure 8. Maps illustrating changes in prairie dog colony boundaries in the experimental treatment and control plots during (a) summer 2002 and (b) summer 2003 for the Peaceful Valley study colony. Colony boundaries were re-mapped each month from May to September in each year. Inset shows study plots in relation to the entire colony.

a) 2002



b) 2003

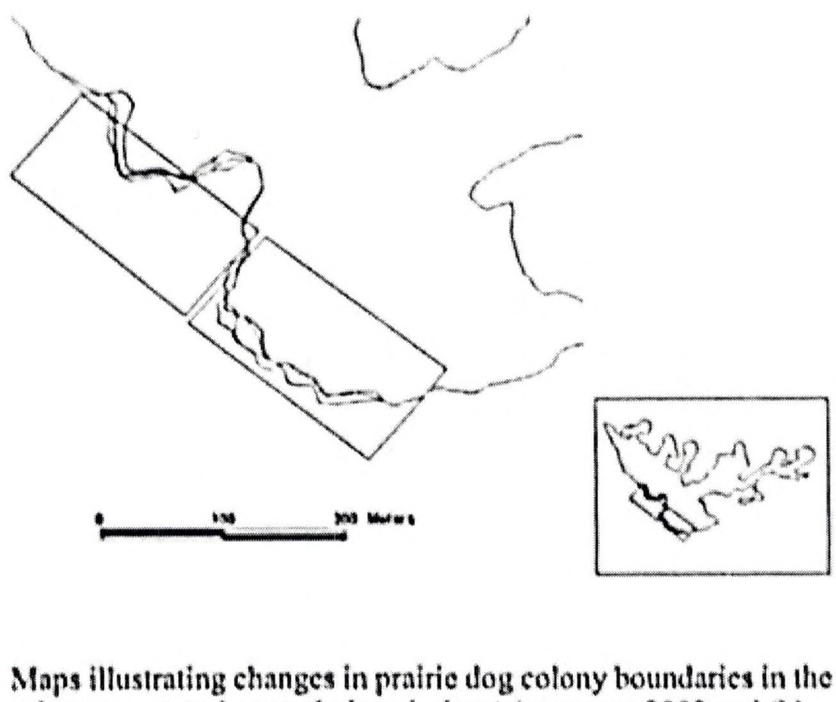
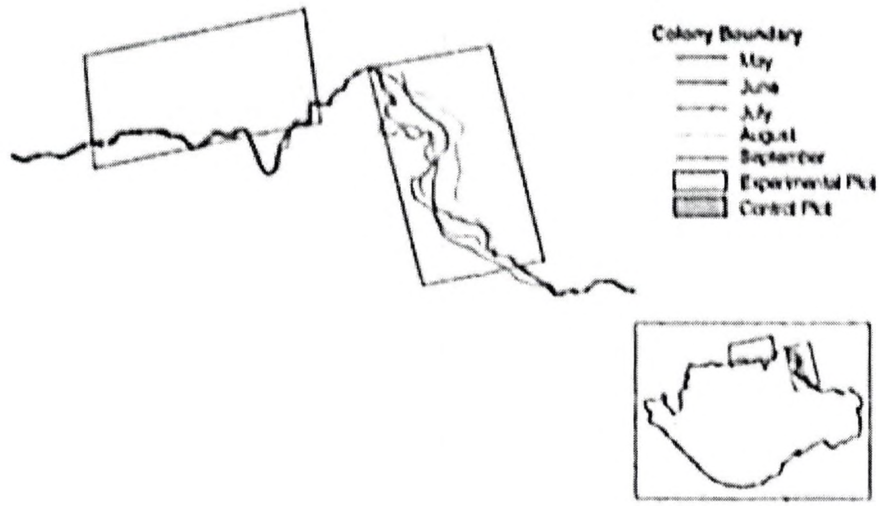


Figure 9. Maps illustrating changes in prairie dog colony boundaries in the experimental treatment and control plots during (a) summer 2002 and (b) summer 2003 for the Mike Auney study colony. Colony boundaries were re-mapped each month from May to September in each year. Inset shows study plots in relation to the entire colony.

a) 2002



b) 2003

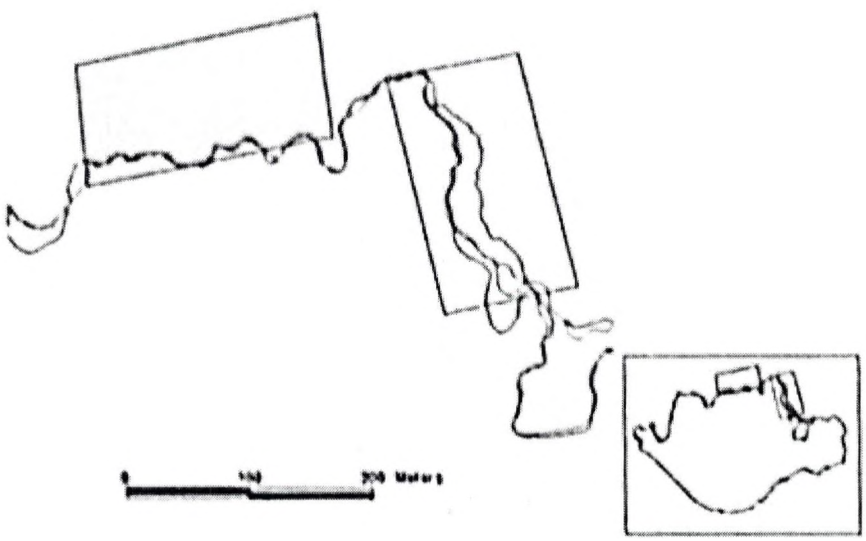


Figure 10. Maps illustrating changes in prairie dog colony boundaries in the experimental treatment and control plots during (a) summer 2002 and (b) summer 2003 for the Johnson's Plateau study colony. Colony boundaries were re-mapped each month from May to September in each year. Inset shows study plots in relation to the entire colony.

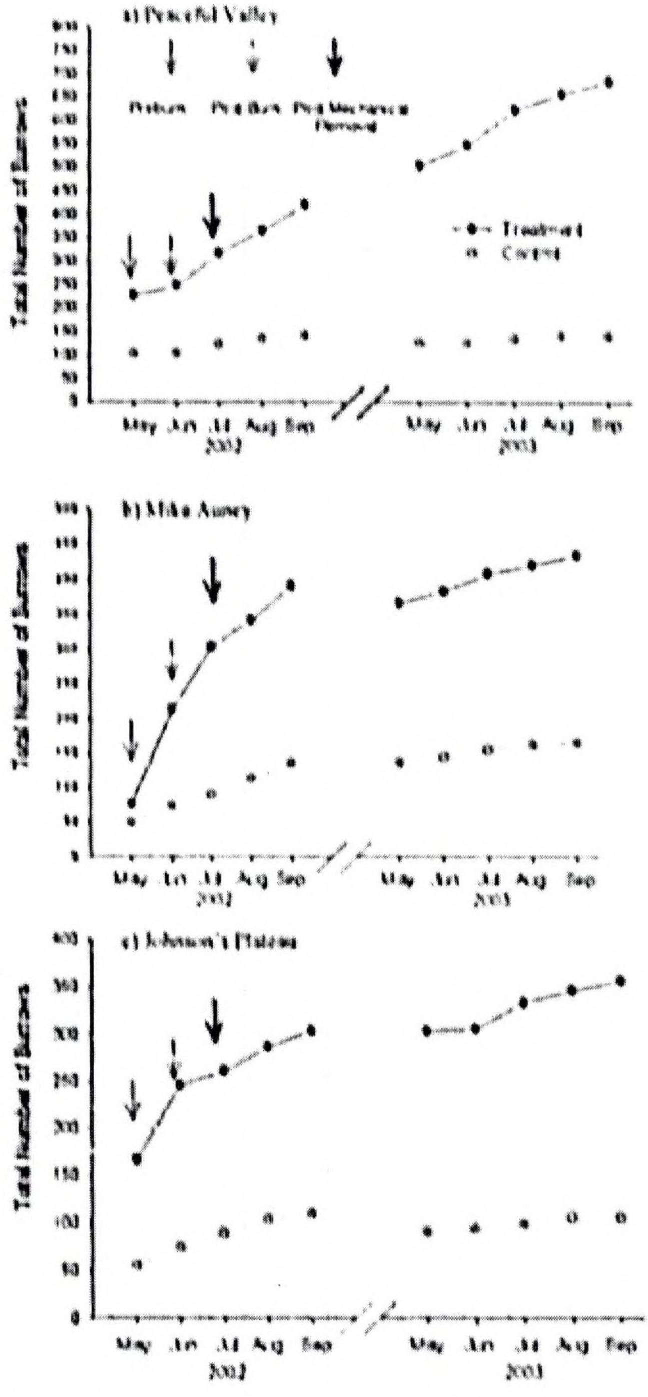


Figure 11. Changes in numbers of prairie dog burrows in the experimental treatment and control plots at the (a) Peaceful Valley, (b) Mike Auney, and (c) Johnson's Plateau study colonies in summer 2002 and summer 2003. Burrow numbers were the total burrows in each area each month during the summer seasons.

2% and 57 ± 11 %, respectively), the overall mean number of prairie dogs observed during summer 2002 was higher in the experimental plots compared to the control plots for the months of July and August but not for June or September (June, $F_{1,4}$ = 0.059, P = 0.820; Jul, $F_{1,4}$ = 11.380, P = 0.043; Aug, $F_{1,4}$ = 51,529, P <0.001; Figure 12 b). In summer 2003 both the actual and adjusted numbers of prairie dogs observed was greater in the experimental plots compared to the control plots (actual, $F_{1,4}$ = 7.519, P = 0.052; adjusted, $F_{1,4}$ = 13.95, P = 0.03; Figure 13). Adjusted counts were based on an average 17 ± 9 % and 57 ± 9 % chance of missing a prairie dog in the experimental treatment and control plots, respectively. I observed higher numbers of prairie dogs foraging and burrowing in the experimental treatment compared to control plots in both 2002 and 2003 (Table 5). I also observed more prairie dogs displaying vigilance in the experimental treatment compared to the control plots (Table 5), which was likely related to the absolute greater numbers of animals using the experimental treatment plots.

Results for behavioral data indicated that prairie dogs foraged, burrowed, and displayed vigilance at higher rates in experimental compared to control plots in both 2002 and 2003 (Table 5). The overall best-fit model that described prairie dog behavior in 2002 included the interactions of town X behavior X treatment (likelihood ratio χ^2 = 342.49, Raftery's BIC = 260.93, $d.f.$ = 8, P < 0.001). Detailed analyses of behavioral data indicated that a higher proportion of prairie dogs foraged (likelihood-ratio χ^2 = 188.19, Raftery's BIC = 168.35, $d.f.$ = 2, P < 0.001), burrowed (likelihood-ratio χ^2 = 81.24, Raftery's BIC = 63.99, $d.f.$ = 2, P < 0.001), and displayed vigilance (likelihood-ratio χ^2 = 6.58, Raftery's BIC = -6.21, $d.f.$ = 2, P = 0.037) in experimental compared to control plots during the summer of 2002 (Table 5). The best log-linear model that described

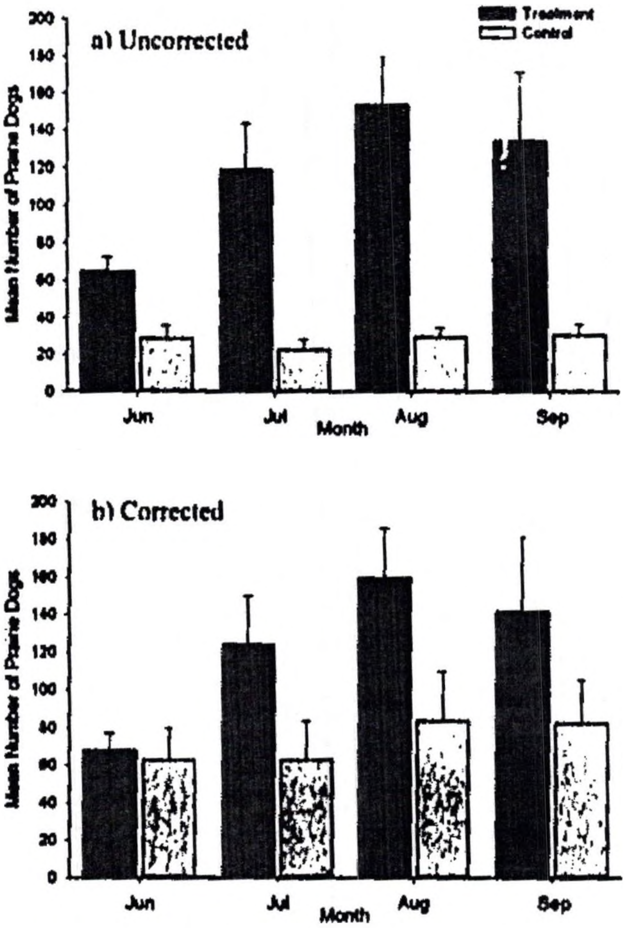


Figure 12. Mean (± SE) number of prairie dogs noted during monthly observation periods in 2002. Data are presented for (a) uncorrected counts, and (b) counts corrected for visual obstruction.

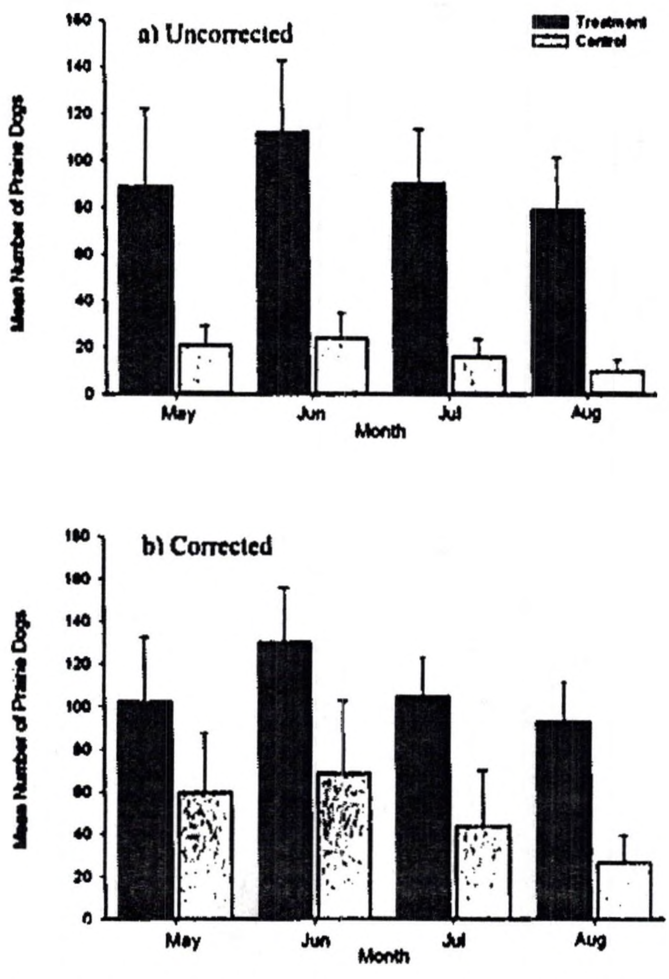


Figure 13. Mean (± SE) number of prairie dogs noted during monthly observation periods in 2003. Data are presented for (a) uncorrected counts, and (b) counts corrected for visual obstruction.

prairie dog behavior in 2003, included the interactions of period × town × behavior × treatment (likelihood-ratio χ^2 = 307.23, Raftery's BIC = 83.36, $d.f.$ = 25, $P < 0.001$), where period was defined by month (period 1 = May-Jul; early in the growing season and period 2 = Aug; late in the growing season). Similarly, additional analysis indicated that a higher proportion of prairie dogs foraged (likelihood-ratio χ^2 = 90.56, Raftery's BIC = 73.09, $d.f.$ = 2, $P < 0.001$), burrowed (likelihood-ratio χ^2 = 20.47, Raftery's BIC = 5.91, $d.f.$ = 2, $P < 0.001$), and displayed vigilance (likelihood-ratio χ^2 = 11.31, Raftery's BIC = 3.03, $d.f.$ = 2, P = 0.003) in the experimental compared to the control plots during the summer of 2003 (Table 5).

Table 5. Summary of data on the numbers of prairie dogs and their behaviors in treatment and control plots at Mike Auney (MA), Peaceful Valley (PV), and Johnson's Plateau (JP) study colonies at Theodore Roosevelt National Park in summers 2002 and 2003. Proportions of time spent performing each behavior is represented in parenthesis.

Plot	Summer 2002			Summer 2003		
type/behavior	MA	PV	JP	MA	PV	JP
Treatment						
Forging	6700(78%)	6764(78%)	3 135(70%)	1659 (82%)	2882 (82%)	851 (82%)
Burrowing	170 (2%)	210 (2%)	171 (3%)	10 (<1%)	52 (2%)	1 (<1%)
Vigilant	1746(20%)	1697(20%)	1 199 27%)	362 (18%)	561 (16%)	189 (18%)
Total	8616	8671	4505	2031	3495	1041
Control						
Forging	1055 (78%)	1746 (76%)	892 (69%)	275 (70%)	521 (73%)	40 (57%)
Burrowing	7 (<1%)	21 (1%)	20 (2%)	2 (<1%)	0 (0%)	4 (6%)
Vigilant	291 (22%)	532 (23%)	368 (29%)	116 (30%)	196 (27%)	26 (37%)
Total	1353	2299	1280	393	717	70

Prairie Dog Density and Abundance

Estimated mean colony density for 2002 was 75.9 ± 30.2 prairie dogs/ha, and 44.7 ± 18.93 prairie dogs/ha for all months surveyed in 2003 (Table 6). Between July 2002 and July 2003 estimated prairie dog density decreased by an average of 59% (64%, 49%, and 65% for Mike Auney, Peaceful Valley, and Johnson's Plateau, respectively), suggesting a consistent downward trend in prairie dog densities between years. In summer 2003 the estimated densities for each colony suggested lower prairie dog numbers compared to summer 2002 (Figure 14). Because density estimates were not based on a mean in 2002, I was unable to quantitatively compare densities between years.

Table 6. Estimated prairie dog densities for the three study colonies at Theodore Roosevelt National Park in 2002 and 2003. Densities were estimated using visual count methods. Means are ± 1 SE.

	Mike Auney		Peaceful Valley		Johnson's Plateau	
Month	2002	2003	2002	2003	2002	2003
June		51.2		23.2		24.3
July	136.2	87.4	42.4	20.7	49.1	31.8
August		108.7		25.7		29.3
Mean		82.4 ± 16.8		23.2 ± 1.5		28.4 ± 2.2

Discussion

This study demonstrated how habitat manipulations designed to enhance habitat quality on the margins of existing black-tailed prairie dog colonies may be used to influence colony expansion. At Theodore Roosevelt National Park, black-tailed prairie dogs responded to the combination of controlled burning and mechanical brush removal by disproportionately greater exploratory movements, foraging, and burrowing activities in treated compared to control areas (Table 5). Overall, these differences in behavior combined to produce highly significant differences in colony expansion into the experimental plots compared to adjacent control plots at all three study colonies (Figure 15). Thus, there was strong support for the idea that habitat manipulations can be used to manage the expansion dynamics of prairie dog colonies by broader scale application of

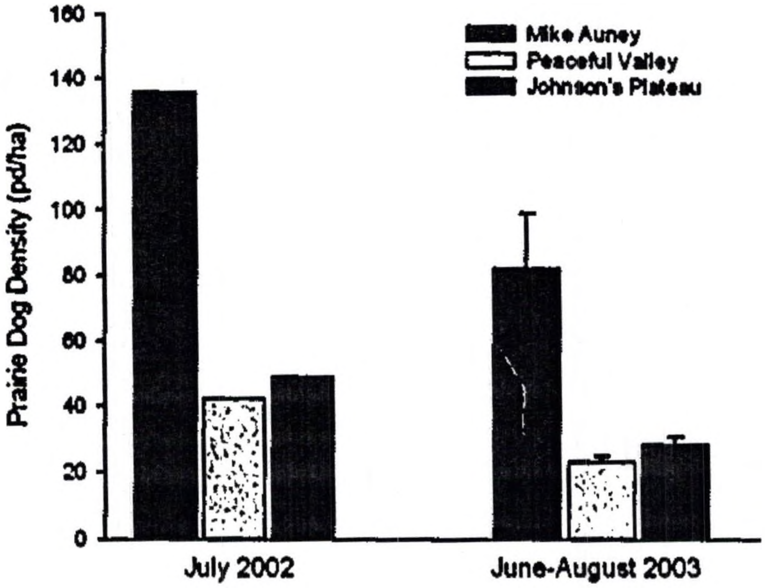


Figure 14. Variation in estimated prairie dog densities at three prairie study colonies in TRNP during summer 2002 and summer 2003. In summer 2002 the density for each colony was estimated from data from a single visual count survey during July. In summer 2003 the density for each study colony was based on the mean for three different visual count surveys conducted (1 survey each for each colony in June, July, and August). Bars are 1 ± SE for summer 2003.

controlled burning or mechanical brush removals around prairie dog colonies. Although the expansion dynamic into experimental plots was consistent and significant among all study colonies, there were differences in the rate of expansion at individual study colonies both within and between years. Weather-induced variation in vegetation appeared important in slowing colony expansion into the experimental plots between years, differences in prairie dog density among study colonies appeared to more importantly influence expansion rates in summer 2002 than summer 2003, and predation was a key factor driving variation in expansion dynamics in summer 2003.

Although all three-study colonies experienced significant expansion into the experimental plots in summer 2002, in summer 2003 colony boundaries were more dynamic, expanding and retracting as vegetative cover fluctuated throughout the growing season. My observations suggested that the combination of a moderate resprouting of shrubs from stumps and a relatively lush growth of green herbaceous plants in the spring to early summer period slowed or halted expansion at the Mike Auney and Peaceful Valley study colonies (Figure 5, 6). The reduction in colony extent in the experimental plot at the Johnson's Plateau colony was entirely related to badger predation, which will be discussed in more detail later. By late summer 2003, foraging by prairie dogs reduced shrub cover and herbaceous plant height in the experimental plots at Mike Auney and Peaceful Valley colonies, when a slow rate of colony expansion was apparent. Although, limited if any expansion occurred in the experimental treatment and control plots, the number of burrows increased in these plots in both years. New burrows were excavated as prairie dogs continued to use the occupied colony edge, old satellite burrows were

Figure 15. Map images illustrating varying extents of total colony expansion (green lines) in the experimental treatment and control plots at the (a) Peaceful Valley, (b) Mike Auney, and (c) Johnson's Plateau prairie dog colonies as of Sep 15, 2003. Black lines represent the initial colony boundaries prior to the burn and mechanical brush removal treatments.

converted to den burrows and new escape burrows were excavated. The lack of any significant expansion into the control plots suggested that when high quality habitat is available, the risks of expanding into areas of poor quality habitat might not outweigh the costs of expansion into those habitats.

Data from prairie dog counts suggested that variation in population density among study colonies contributed to important differences in expansion into experimental plots during summer 2002, but not necessarily in summer 2003. During summer 2002, the Mike Auney prairie dog colony supported slightly more than three times the density of prairie dogs as either the Johnson's Plateau of Peaceful Valley study colonies (Table 5). Colony expansion into the Mike Auney experimental plot in 2002 was estimated at 1.26 ha (74% of area available for expansion) compared to expansions of 0.62 ha (36% of area available for expansion) and 0.89 ha (40% of area available for expansion) into the experimental plots at the Johnson's Plateau and Peaceful Valley study colonies, respectively. Estimated prairie dog densities were lower for all three study colonies in summer 2003 compared to summer 2002 (Table 6), which may have contributed to the reduced expansion into experimental plots in 2003. Notably, however, the Mike Auney colony continued to harbor nearly twice the density of prairie dogs as the other two colonies in summer 2003 (Table 6), suggesting that density alone does not drive colony-level expansion. Prairie dogs are a colonial species that relies on the presence of conspecifics to maintain suitable habitat and to facilitate successful anti-predator vigilance. Increased numbers of prairie dogs may only be beneficial to prairie dog fitness when competition for forage is low (Stephens et al. 1999). For example, in drought years, when food resources are scarce and population density is high, increased competition for resources forces prairie dogs to expand into areas of suitable habitat at colony peripheries in search of food. In years of above average rainfall, food resources will be more abundant, thereby reducing competition within colony boundaries and eliminating the need to search for food at the colony edge.

Predation by badgers and not forage availability or population density was an important factor that limited colony expansion at the Johnson's Plateau study colony in summer 2003. At the Johnson's Plateau study colony a pair of badgers moved into the experimental plot sometime in early 2003, dramatically changing expansion dynamics at that colony between 2002 and 2003. The two badgers excavated and used the mounds around five presumed den burrows to loaf and monitor prairie dog movements. On several occasions I observed the badgers charge from one of these mounds and begin digging into the burrows of fleeing prairie dogs. Overall, one or both of the badgers was observed in the experimental plot on 23 of the 29 days that behavioral observations were conducted at the Johnson's Plateau study colony. The presence of a resident pair of badgers on the Johnson's Plateau study colony caused a sharp decline in prairie dog activity in the experimental study plot, ultimately resulting in reduced colony expansion into the plot in summer 2003 compared to summer 2002 (Figure 7, Table 3). In other areas badgers have been noted to preferentially hunt along the peripheries of prairie dog colonies where prairie dogs may be more vulnerable to predation (Koford 1958).

Although circumstances required the use of a combination of controlled burning and mechanical brush removal at the experimental study colonies, I believe that either method alone would have been sufficient to influence colony-level expansion dynamics. Daubenmire (1968) for example, noted that either controlled burns or mechanical brush removals can dramatically reduce vegetation height and cover of shrubs and woody plants, which appear to be the proximate cue prairie dogs use to assess the suitability of habitat in terms of their ability to detect approaching predators. More recently, and as part of a yet to be published experiment, Ford et al. (2003) reported that black-tailed prairie dogs responded similarly to burn and mowing treatments at the population level. This study did not track changes in colony boundaries, however.

The original hypothesis that prairie dogs would forage and burrow proportionately more in the experimental plots, with an increased occurrence of vigilant behavior in the control was not fully supported. Reconsidering the hypothesis, an increased occurrence of vigilant behavior in experimental plots was not unexpected. Prior to expansion, prairie dogs explore and assess potential habitat by observing (being vigilant) their surroundings. Moreover, dispersing prairie dogs may be more vulnerable to predation as they usually disperse alone and along the colony periphery away from the most active part of the colony were prairie dogs can rely on conspecifics to detect predators. Hoogland (1979) noted that prairie dog alertness correlates with their position on the colony; individual alertness increases as prairie dogs approach the colony's edge and decreases as prairie dogs move inwards toward the colony center. Therefore, although vegetative cover was reduced (increasing visibility and the chance of detecting predators), prairie dogs were expanding into unfamiliar territory; usually without the company of conspecifics and thus vigilant behavior may have been increased to enhance survival.

The ability to initiate colony expansion by manipulating habitat conditions near colony boundaries such that habitat is improved and made suitable for colony expansion has important conservation and management implications. Because black-tailed prairie dogs are a candidate species for protection under the Endangered Species Act, many state and federal management agencies are interested in recovering and maintaining viable prairie dog populations. Encouraging the growth and expansion of prairie dog colonies by removal of shrub and plant cover may aid in the restoration and expansion prairie dogs in areas where colonies have been reduced or eliminated. Additionally, because prairie dogs are considered a keystone, species restoring prairie dog populations will increase habitat for their many associated species, including the black-footed ferret.

CHAPTER 3

HABITAT SUITABILITY MODELING AS A TOOL FOR MANAGING PRAIRIE DOGS IN WESTERN NORTH DAKOTA

"Prairie-dogs are abundant...; they are in shape like little woochucks, and are the most noisy and inquisitive animals imaginable. They are never found singly, but always in towns of several hundred inhabitants; and these towns are found in all kinds of places where the country is flat and treeless."

--- Theodore Roosevelt

Introduction

The black-tailed prairie dog (*Cynomys ludovicianus*) is a highly social polygynous rodent that lives in colonies consisting of a matrix of burrows and underground tunnels (Hoogland 1995). Black-tailed prairie dogs are herbivores that feed on a variety of grasses and forbs (Kotford 1958). The foraging activities of prairie dogs decreases plant height and alters plant species composition (Coppock et al. 1983,Cincotta et al. 1989), which in combination with burrowing activities, alters rates of nitrogen uptake in plants and increases nutrient availability to larger herbivores (Wydeven and Dahlgren 1984). Over time these activities create mosaics of habitat that vary in vegetation structure and plant species composition that contributes to increased habitat heterogeneity in short and mixed-grass prairie ecosystems (Coppock and Detling 1986, Weltzin et al. 1997). Many plants and animals benefit by the activities of black-tailed prairie dogs and the species is considered a keystone species because of its disproportionate effect on the composition, integrity, and function of prairie communities (Kotliar et al. 1999).

The historic range of black-tailed prairie dogs encompassed most of North America's short and mixed-grass prairies. However, during the 1800s and 1900s the species was greatly reduced in number and range by extensive habitat loss and persecution, primarily associated with agricultural development ultimately affecting species diversity and prairie ecosystem dynamics. As a result, black-tailed prairie dogs are of important management interest related to their importance as a keystone species and their conservation status as a candidate species under the Endangered Species Act. Because the species is a candidate for listing as a threatened or endangered species, many state and federal agencies are interested in reliable information regarding prairie dog populations including habitat requirements, habitat suitability, and other natural or human-related factors impinging on the recovery and maintenance of viable populations of prairie dogs. In an effort to aid in the management and recovery of black-tailed prairie dogs, I developed a Geographic Information System (GIS) based Habitat Suitability Index (HSI) model for black-tailed prairie dogs in western North Dakota using data on habitat attributes associated with the species.

Habitat suitability index models are simplifications of real-world systems that provide a framework around which qualitative and quantitative habitat relationships can be structured into testable hypotheses for wildlife management decision-making (Schamberger and O'Neil 1986). In recent years HSI models have become important tools for science-based management of wildlife and their habitats. Without proper validation, however, HSI models can be misleading and misused. Testing HSI models is therefore critically important for providing information about model performance and reliability for model improvement (Schamberger and O'Neil 1986).

The model integrated information on vegetation, slope, proximities to nearby colonies, and landownership (federal, state, private) to identify areas of suitable habitat for prairie dogs. I tested or validated the reliability of the model for identifying suitable habitats for the species by testing the assumption that a species-habitat relationship exists between high quality habitat and habitat preference by prairie dogs, and by evaluating the ability of the HSI model to identify habitats currently occupied by prairie dogs.

Habitat Associations and Potential Limiting Factors for Black-Tailed Prairie Dogs

Basic habitat attributes thought to influence habitat selection by prairie dogs include vegetation, soil type, and slope (Koford 1958). Prairie dogs prefer areas with sparse vegetation (Merriam 1902), and relatively low growing vegetation (7 to 13 cm in plant height; Koford 1958, Clark et al. 1982, Agnew et al. 1986). Low vegetative cover improves the ability of prairie dogs to detect predators (Hoogland 1995). Prairie dogs may also colonize or expand into areas that have been heavily grazed or disturbed (Reid 1954), and they are known to avoid foraging in tree stands and shrub-dominated areas where their ability to detect predators is compromised (Koford 1958). Given enough time, however, prairie dogs are able to expand into sagebrush (*Artemisia* spp.)/shrub-dominated areas by gradually uprooting plants growing near the periphery of existing colonies (Osborn 1942).

Prairie dog colonies with their extensive burrow systems may be associated with a variety of soils as long as the soils are capable of supporting stable burrow systems (Koford 1958). In general, prairie dogs avoid establishing colonies in areas with fine sandy soils, and in low lying areas along rivers and streams that are exposed to extensive seasonal flooding (Koford 1958). In the Great Plains, prairie dog colonies are typically associated with fine to medium textured alluvial soils (Reid 1954, Koford 1958, Knowles 1986). In North Dakota, prairie dog colonies are found on clay loam soils on benches above rivers and on upland plateaus (Reid 1954). Although prairie dogs are considered to prefer loamy soils, high-density populations may expand into areas where soils are predominately clay or soft lignite (Kotford 1958). My review of the literature suggests that prairie dogs are generally not limited by soil type. Rather, the texture of soils and the influence of texture on soil moisture and vegetation may be more important in determining prairie dog presence (Koford 1958).

Colonies of black-tailed prairie dogs have been observed across a wide range of slopes throughout their distributional range. In general, however, prairie dogs avoid flat or low-lying areas subject to seasonal flooding and areas with steep slopes and complex topographies (Koford 1958). In other regions it has been suggested that the optimal slope range for prairie dog colonies is 0 to 15% (Koford 1958, Tileston and Lechleitner 1966, Knowles 1986, Clippinger 1989, and Reading and Matchett 1997). In North Dakota, prairie dogs are infrequently found on slopes greater than 25% (Reid 1954).

Study Area

The Little Missouri National Grasslands is located along the Little Missouri River corridor, an area characterized by flat plateaus, rugged canyons, and alluvial benches associated with the Little Missouri River and its tributaries. The Little Missouri National Grasslands are divided into two districts, the Medora Ranger District in the south and the McKenzie Ranger District in the north, together encompassing 415,929 ha of intermingled federal, state and private land. Theodore Roosevelt National Park is composed of three units, the North Unit (9,738 ha), South Unit (18,663 ha) and the Elkhorn Ranch Unit (88 ha), all entirely within the Little Missouri National Grasslands. A total of 189 prairie dog colonies are located in the Little Missouri National Grasslands (119 in the Medora Ranger District and 70 in the McKenzie Ranger District; Knowles 2003), whereas the North and South Units of Theodore Roosevelt National Park contain 20 and three prairie dog colonies, respectively. The Elkhorn Ranch Unit of Theodore Roosevelt National Park does not contain any colonies. Total colony areas are estimated at 2,364 ha for the Little Missouri National Grasslands (1,656 ha in the Medora Ranger District and 708 ha in the McKenzie Ranger District) and 498 ha for Theodore Roosevelt National Park (59 ha in the North Unit and 439 ha in the South Unit).

Vegetation in the region is dominated by western wheatgrass (*Agropyron smithii*), blue grama (*Bouteloua gracilis*), little bluestem (*Schizachyrium scoparium*) and silver sagebrush (*Artemisia cana*) on the rolling hills and prairies, rocky mountain juniper (*Juniperus scopularum*) and green ash (*Fraxinus pennsylvanica*) along the woody draws, and eastern cottonwood (*Populus deltoides*) along the river. Soils belong to the Bainville Series, developed from excessively drained medium-texture, calcareous parent material. Elevation ranges from 550 to 1,070 m throughout the study sites. The climate is characterized as semi-arid with long cold winters and short hot summers; temperatures range from an average low of −11.6 °C in January to an average high of 22 °C in July. Average annual rainfall is 380 mm, with most precipitation falling in early summer (May and June).

Methods

I used information on vegetation, slope, proximities to nearby colonies, and landownership (federal, state, private) to develop a series of HSI models for use in identifying areas of suitable habitat for prairie dogs. Habitat suitability was estimated based on the assumptions that prairie dogs respond more favorably to areas dominated by low growing vegetation and relatively low slopes than areas dominated by shrubs, and they avoid habitats on steep slopes dominated by trees. Additionally, because black-tailed prairie dogs are highly social and colonial (Hoogland 1995), I assumed that new colony establishment would be related to dispersal by prairie dogs from existing neighboring colonies such that areas close to existing colonies represented areas of higher quality habitat than areas further from occupied colonies. Soil type was not used in the model because studies have found that soil was a less important determinant of habitat use by prairie dogs than vegetation or slope (Proctor 1998).

I developed several different types of HSI models for Theodore Roosevelt National Park and the Little Missouri National Grasslands including a "basic habitat model", an "effective dispersal model", a "maximum dispersal model" and a "landownership model" (Little Missouri National Grasslands only). A landownership model was not developed for Theodore Roosevelt National Park because the park is entirely federally owned, rather than a mix of public and private lands. The basic habitat models integrated information on vegetation class (Table 7) and slope categories (Table 8) for the park and national grassland areas. The effective dispersal distance models incorporated vegetation class, slope category, and information on the estimated effective dispersal distance of prairie dogs (defined and detailed below). Maximum dispersal distance models incorporated data on vegetation class, slope category, and estimated maximum dispersal distances. The landownership model incorporated data on vegetation class, slope category, and public and private landownership for the Little Missouri National Grasslands.

Habitat suitability was determined by assigning each environmental variable (V_1= vegetation class, V_2 = slope category, V_3 = effective dispersal distance, V_4 = maximum dispersal distance, and V_5 = landownership) a suitability index (SI) score based on that variable's importance in defining preferred prairie dog habitat, where highly preferred habitat attributes received a higher SI score than less preferred attributes. Suitability index scores were assigned based on knowledge of the life history of black-tailed prairie dogs, attributes of their distribution from the literature, and analyses of existing prairie dog colonies at several national parks in the region. Habitat suitability was then defined by combining SI values in the following equation:

$$HSI = ((SIV_1)(SIV_2)\ldots). \tag{1}$$

The above equation expresses that prairie dog preference for habitat increases with increasing HSI values based on the assumptions that (1) prairie dogs respond to increased habitat quality, (2) the entire range of prairie dog occurrence is taken into account, (3) prairie dogs have an unobstructed use of their habitat, and (4) that the population of prairie dogs modeled represents an unharvested population (Thomasma et al. 1991).

Habitat Classification

Vegetation data for Theodore Roosevelt National Park and the Little Missouri National Grasslands were obtained as 1:24,000 digital databases developed by the

NBS/NPS vegetation-mapping program and the USDA Forest Service (National Park Service and USDA Forest Service, Northern Region 2002). Vegetation information/layers for the park included approximately 40 different vegetation alliances whereas vegetation layers for the Little Missouri National Grasslands were grouped into 34 different dominance types/current life form groupings. I used a combination of data on dietary preferences of prairie dogs and plant physiognomy to reclassify the multiple vegetation layers into nine vegetation classes for Theodore Roosevelt National Park and the Little Missouri National Grasslands, respectively (Table 7). The nine vegetation classes were then assigned suitability index scores for use in the HSI models (Table 7).

Information on vegetation type/alliance was not available for colony areas currently occupied by prairie dogs at Theodore Roosevelt National Park. Therefore, interpolation techniques were used to estimate habitat types in areas currently occupied by prairie dog colonies based on vegetation around colony peripheries. Prior to interpolation, I created a vegetation layer without prairie dog complexes, and merged that layer with an older vegetation layer, where prairie dog complexes were smaller, thus minimizing unknown area and increasing the accuracy of interpolation. Inverse distance weighting methods were used to reconstruct what vegetation would have potentially occupied each colony prior to colonization or expansion. Inverse distance weighting is an interpolator that assumes each measured point within a neighborhood has a local influence on an unknown point, which diminishes with distance. Inverse distance weighting was performed using the GeoStatistical Analyst module of ArcGIS 8.3 (ESRI, Redlands, CA), where each observed point within a neighborhood of five cells was assigned a weighted power of 4.58 (determined in GeoStatistical Analyst), used to control the influence that point has on the interpolated surface. The greater the weighting power, the less influence points far from the interpolated point have on the final output. Vegetation information for the prairie dog colonies in the Little Missouri National Grasslands was already available and interpolation was not needed for this area.

Table 7. Summary of HSI rankings for different habitat types at TRNP and the LMNG. Vegetation was derived from GIS data layers provided by the USDA Forest Service and National Park Service, 2002.

TRNP		LMNG	
SI Score	Habitat Type	SI Score	Habitat Type
0	Water, Roads, Badlands	0	Water, Roads, Bare Soil
10	Coniferous Trees/Shrubs	10	Agriculture
15	Temporarily Flood Deciduous Trees	20	Coniferous Trees/Shrubs
20	Deciduous Trees	30	Broadleaf Trees
30	Exotic Species	35	Broadleaf Trees/Shrubs
40	Tall Shrubs	40	Broadleaf Trees/Graminoid
45	Temporarily Flood Shrubs	50	Shrubs
50	Shrubs	55	Shrubs/Graminoid
60	Herbaceous/Grass	60	Herbaceous/Graminoid

I obtained elevation data as 30 m x 30 m Digital Elevation Models from the United States Geological Survey (USGS). Percent slope was calculated using Spatial Analyst in ArcGIS 8.3 (ESRI, Redlands, CA). I defined slope preference by prairie dogs using occupancy data from six regional national parks (Badlands, Theodore Roosevelt and Wind Cave National Parks, Devil's Tower and Scott's Bluff National Monuments, and Bent's Old Fort National Historic Site). Analyses of extant prairie dog colonies suggests that the black-tailed prairie dogs prefer areas averaging 7% slope (range = 0.5 to 31% based on 95% confidence intervals). Based on these data six different slope categories were defined for HSI modeling (Table 8).

Table 8. Summary of HSI rankings for percent slope at TRNP and the LMNG. Data were derived from 30 m x 30 m Digital Elevation Models determined by the USGS.

SI Score	Percent Slope
0	>25%
5	20-25%
10	15-20%
30	10-15%
50	5-10%
60	0-5%

Among socially polygnous mammals including prairie dogs, dispersal is typified by young of the year or yearling males leaving their natal territories to settle and establish breeding positions elsewhere (Michener 1983). Detailed studies of dispersal behavior in black-tailed prairie dogs are limited (Hoogland 1981), but maximum dispersal distances for the species have been estimated at around 3,200 m (Knowles 1985, Garrett and Franklin 1988, Hoogland 1995). It is not clear, however, how maximum individual dispersal distances relate to the actual formation of new colonies of prairie dogs (effective dispersal distance). I assumed that new colonies are formed by dispersing prairie dogs from nearby colonies and defined the effective dispersal distance for prairie dogs as the straight-line distance between the centroids of newly established colonies and the nearest neighboring colony. Data used to estimate effective dispersal distance were based on historical and recent maps of prairie dog colonies at Theodore Roosevelt National Park, the Little Missouri National Grasslands, Badlands National Park, and Scott's Bluff National Monument. All recent and historic prairie dog colonies were entered into a GIS as polygons from which centroid points were calculated. Using the Nearest Neighbor Extension (Weigel 1992) for ArcView 3.1 (ESRI, Redlands, CA), I measured the straight-line distance between the centroids of a newly established colony and the nearest established colony. Based on 120 newly established colonies between 1977 and 2003, the average effective dispersal distance was 1,800 m ± 165 m. Two models were then created, one with a 1,800 m buffer around established colonies capturing the effective dispersal distance, and a second with a 3,200 m buffer around established colonies capturing the maximum dispersal distance.

Land ownership may be an important predictor of habitat quality for prairie dogs in the Little Missouri National Grasslands where public and private lands are intermixed. Research by Knowles (2003) suggests that prairie dog colonies located on private lands in North Dakota are more likely to be subject to poisoning than colonies on public lands (Knowles and Hagen 2003). I therefore created a model for the Little Missouri National Grasslands that assigned private lands SI values of zero, effectively minimizing the importance of private lands for future prairie dog management by state and federal entities. Notably, this does not imply that prairie dogs will be eliminated from private lands, only that active management and conservation measures will be focused around public lands.

Model Validation

Models were validated by testing the assumption that a correlation exists between increasing SI scores and habitat quality, and by assessing how well different models performed in predicting prairie dog locations at Theodore Roosevelt National Park and the Little Missouri National Grasslands. I tested the assumption that the preference for prairie dogs for habitats varying in slope and vegetation increased with increasing SI values. The preference index was calculated as:

PI = (% occupied habitat within a HSI class)/
(% available habitat within a HSI class). (2)

Analyses included a linear regression of SI and PI values, and χ^2 goodness of fit test of the number of cells of different SI values that were occupied compared to availability. When comparing models, I used the Raftery's Bayesian Information Criterion (BIC) to identify the best-fit model. The model with the lowest BIC is assumed to be the most parsimonious model and thus the model that best describes how prairie dogs utilize available habitats (SYSTAT 8.0, 1998). Model validation was preformed on all relevant combinations of model parameters except landownership. Because habitats on private lands were given a zero HSI ranking for sociological rather than biological reasons, model validation was not performed on models including landownership. All statistical analyses were completed using SYSTAT 8.0 statistical software package (SPSS Inc., Chicago, IL).

Results

Overall Model Results

Each model was unique in its definition of preferred prairie dog habitat, therefore the locations and quantity of suitable habitat varied among models (Table 9). At Theodore Roosevelt National Park, the basic habitat model identified 34% of available habitat as highly suitable (Figure 16; Table 9). Based on the effective and maximum dispersal models, 20% and 35% of available habitat was identified as highly suitable for prairie dogs, respectively (Figure 17, 18; Table 9). In the Little Missouri National Grasslands the simple habitat model identified 57% of available habitat as highly suitable, eleven %

and 24% of available habitat in the Little Missouri National Grasslands was identified as highly suitable for prairie dogs based on the effective and maximum dispersal habitat models, respectively (Figure 19, 20, 21; Table 9). In the landownership model, the amount of highly suitable habitat available for prairie dogs in the Little Missouri National Grasslands was reduced to 31% from 57% in the basic habitat model (Figure 22; Table 9).

Performance of Model Parameters

A positive species-habitat relationship existed between high quality habitat and habitat preference by prairie dogs. There was a positive correlation between habitat preference and highly ranked vegetation at Theodore Roosevelt National Park ($r^2 = 0.687$, $P = 0.006$; Figure 23a), even though prairie dogs used HSI class zero more than expected. Similarly, for the Little Missouri National Grasslands, I detected a positive overall relationship with high quality habitats ($r^2 = 0.573$, $P = 0.018$; Figure 23b) and a higher than expected preference for HSI classes 0 and 10. A positive correlation between high SI values for slope and prairie dog presence was also noted at Theodore Roosevelt National Park ($r^2 = 0.773$, $P = 0.021$; Figure 24a) and the Little Missouri National Grasslands ($r^2 = 0.870$, $P = 0.007$; Figure 24b). When vegetation and slope were compared individually, vegetation appeared more important in explaining habitat preference than slope at both Theodore Roosevelt National Park (vegetation; likelihood ratio $\chi^2 = 1,433$, Raftery's BIC = 1,334, *d.f.* = 9, $P < 0.001$ and slope; likelihood ratio $\chi^2 = 4,060$, Raftery's BIC = 3,997, *d.f.* = 5, $P < 0.001$) and the Little Missouri National Grasslands (vegetation; likelihood ratio $\chi^2 = 8,186$, Raftery's BIC = 8,058, *d.f.* = 8, $P <$

Table 9. Estimated area (ha) of available habitat in high, intermediate, and low areas of habitat suitability at Theodore Roosevelt National (TRNP) and in the Little Missouri National Grasslands (LMNG) based on various HSI models.

	Basic Model		Effective Dispersal Distance Model		Maximum Dispersal Distance Model		Landownership Model
Habitat Suitability[1]	TRNP	LMNG	TRNP	LMNG	TRNP	LMNG	LMNG
High	9,656 (34%)[2]	237,080 (57%)[2]	5,680 (20%)	45,752 (11%)	9,940 (35%)	99,823 (24%)	128,938 (31%)
Intermediate	5,112 (18%)[2]	95,664 (23%)	9,088 (32%)	216,283 (52%)	7,668 (27%)	19,9646 (48%)	41,593 (10%)
Low	13,632 (48%)[2]	83,186 (20%)	13,632 (48%)	153,894 (37%)	10,792 (38%)	11,6460 (28%)	245,398 (59%)

[1] Areas defined with high habitat suitability are composed of HSI classes 8-10, areas of intermediate habitat suitability are composed of HSI classes 4-7, and areas with low habitat suitability are composed of HSI class 1-3.

[2] Percent of the total area of habitat available to prairie dogs at Theodore Roosevelt National Park and in the Little Missouri National Grasslands.

0.001). Analysis of standard deviations between observed verses expected habitat occupation suggests prairie dogs preferentially choose habitats characterized by 0-5% slope dominated by graminoids, and avoid slopes greater than 25% and woodlands dominated by juniper and broadleaf trees at Theodore Roosevelt National Park and in the Little Missouri National Grasslands, respectively (Figures 23, 24).

Individual Model Performance

Prairie dogs used areas of high quality habitat more than expected based upon availability for all models. The basic habitat model performed better at Theodore Roosevelt National Park (likelihood ratio $\chi^2 = 3{,}733$, Raftery's BIC = 3,619, *d.f.* = 9, $P < 0.001$; Figure 16) than in the Little Missouri National Grasslands (likelihood ratio $\chi^2 = 18{,}748$, Raftery's BIC = 18,603, *d.f.* = 9, $P < 0.00$; Figure 19). At Theodore Roosevelt National Park the model including vegetation, slope and maximum dispersal distance (likelihood ratio $\chi^2 =$ 3,185 Raftery's BIC = 3,069, *d.f.* = 9, $P < 0.001$; Figure 18) performed better than the model including vegetation, slope and effective dispersal distance (likelihood ratio $\chi^2 =$ 6,395, Raftery's BIC = 6,281, *d.f.* = 9, $P < 0.001$; Figure 17). For the Little Missouri National Grassland, the maximum dispersal distance model performed better (likelihood ratio $\chi^2 = 43{,}015$, Raftery's BIC = 42,871, *d.f.* = 9, $P < 0.001$; Figure 21) than the effective dispersal distance model (likelihood ratio $\chi^2 = 49{,}551$, Raftery's BIC = 49,406 *d.f.* = 9, $P < 0.001$; Figure 20). Nevertheless, the best performing model for the Little Missouri National Grassland included only vegetation and slope (Figure 19).

Discussion

Analysis of model parameters and model performance support the validation of HSI models proposed for prairie dogs in western North Dakota. Prairie dogs were found to

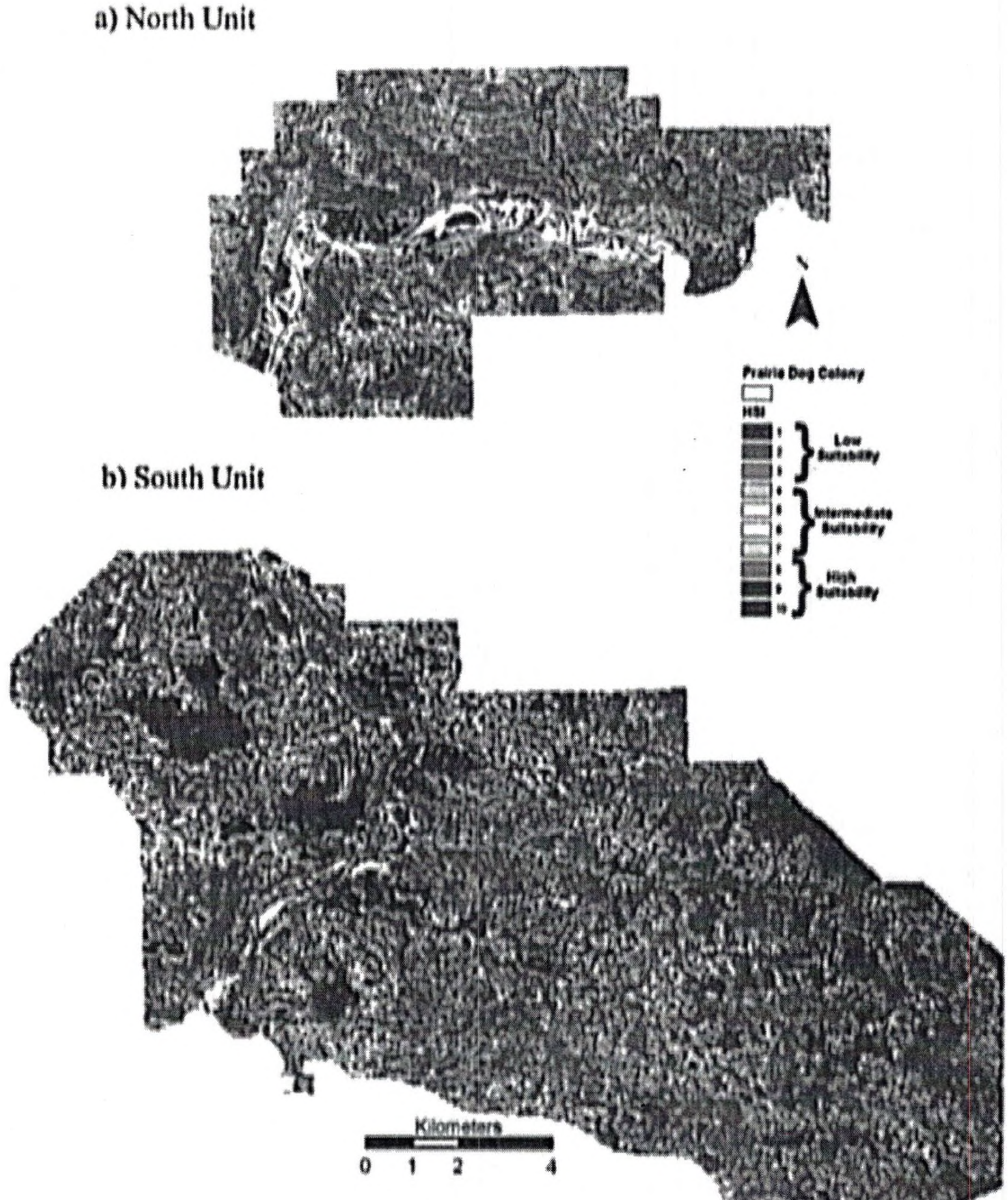


Figure 16. Output of the basic habitat suitability model that integrated data on vegetation and slope for characterizing the suitability of the (a) North Unit and (b) South Unit of Theodore Roosevelt National Park, North Dakota for black-tailed prairie dogs. Habitat suitability index rankings were grouped into three classes (low, intermediate, high) for estimating the total areas by suitability class. Data on estimated areas of habitat within each suitability class are summarized in Table 9.

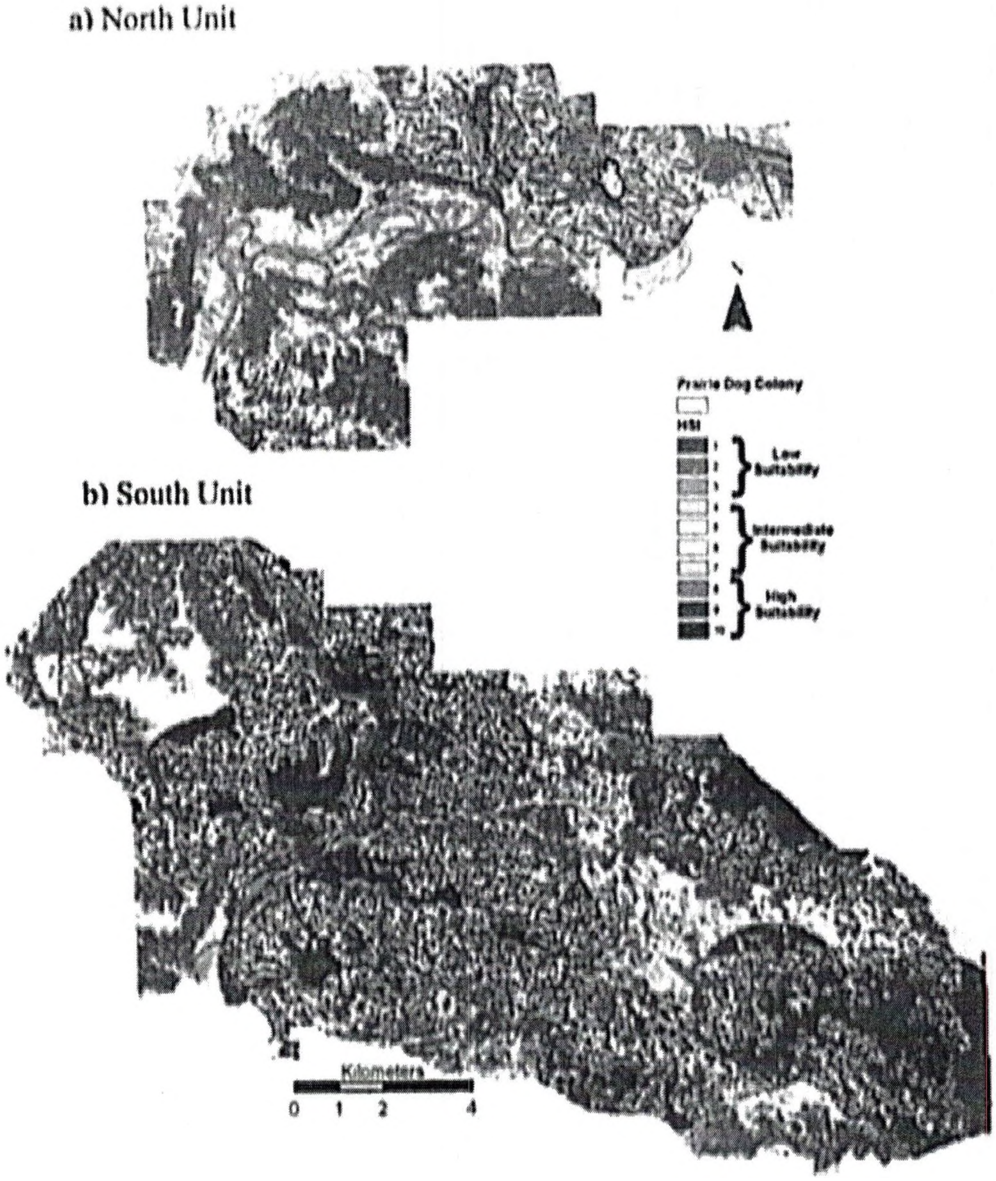


Figure 17. Output of the effective dispersal distance habitat suitability model that integrated data on vegetation, slope, and effective dispersal distance for characterizing the suitability of the (a) North Unit and (b) South Unit of Theodore Roosevelt National Park, North Dakota for black-tailed prairie dogs. Habitat suitability index rankings were grouped into three classes (low, intermediate, high) for estimating the total areas by suitability class. Data on estimated areas of habitat within each suitability class are summarized in Table 9.

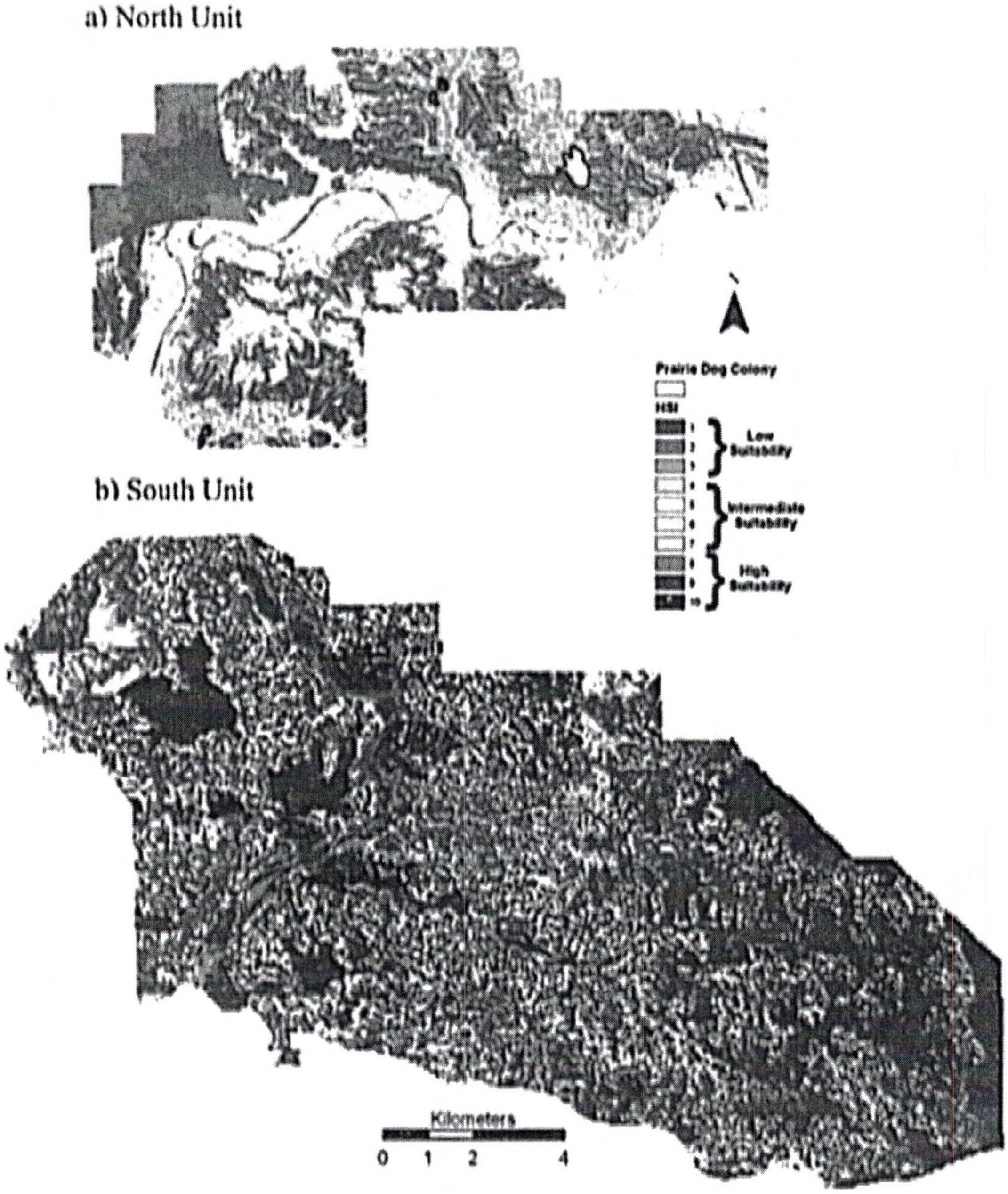


Figure 18. Output of the maximum dispersal distance habitat suitability model that integrated data on vegetation, slope, and maximum dispersal distance for characterizing the suitability of the (a) North Unit and (b) South Unit of Theodore Roosevelt National Park, North Dakota for black-tailed prairie dogs. Habitat suitability index rankings were grouped into three classes (low, intermediate, high) for estimating the total areas by suitability class. Data on estimated areas of habitat within each suitability class are summarized in Table 9.

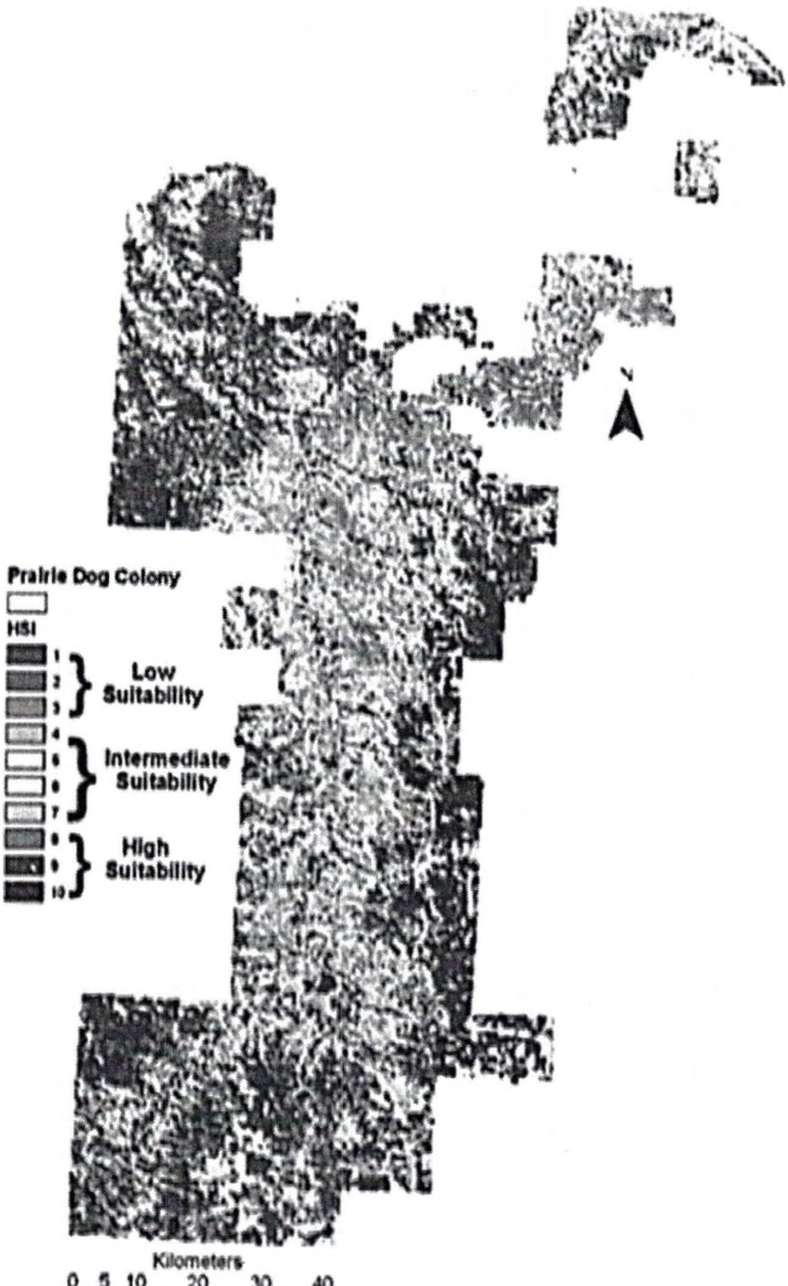


Figure 19. Output of the basic habitat suitability model that integrated data on vegetation and slope for characterizing the suitability of the Little Missouri National Grasslands for black-tailed prairie dogs. Habitat suitability index rankings were grouped into three classes (low, intermediate, high) for estimating the total areas by suitability class. Data on estimated areas of habitat within each suitability class are summarized in Table 9.

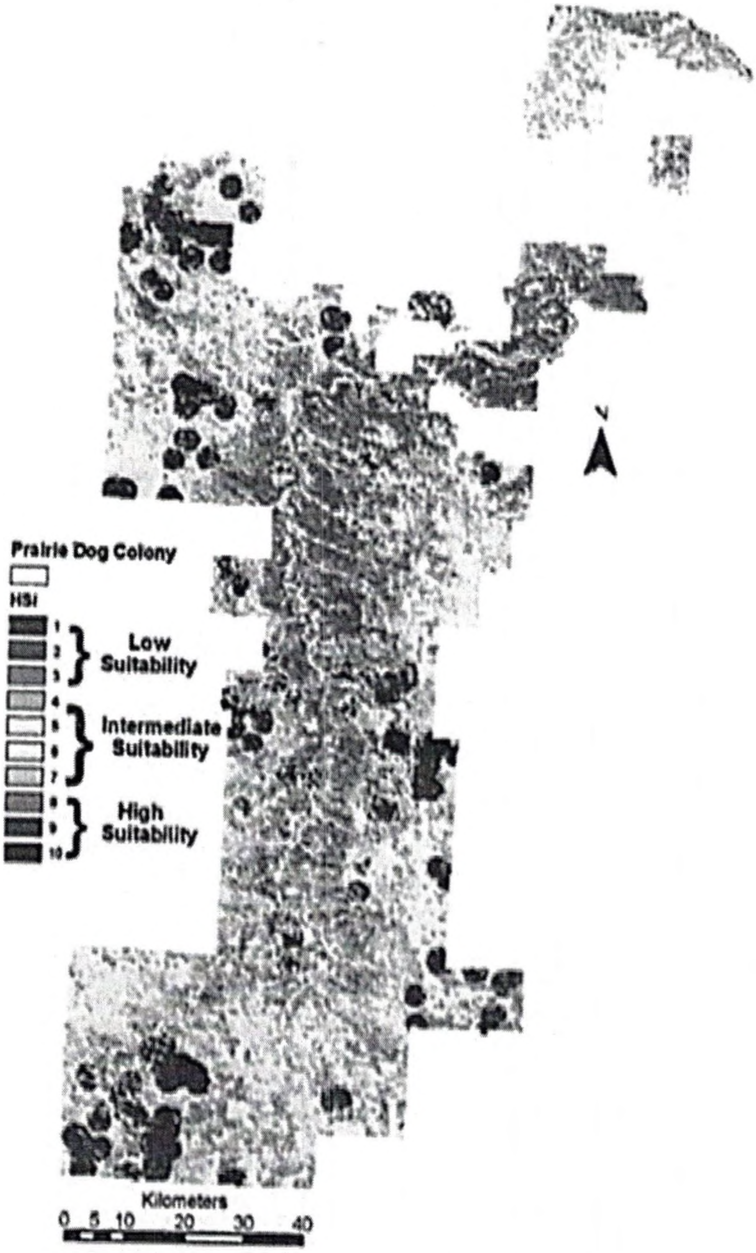


Figure 20. Output of the effective dispersal distance habitat suitability model that integrated data on vegetation, slope, and effective dispersal distance for characterizing the suitability of the Little Missouri National Grasslands for black-tailed prairie dogs. Habitat suitability index rankings were grouped into three classes (low, intermediate, high) for estimating the total areas by suitability class. Data on estimated areas of habitat within each suitability class are summarized in Table 9.

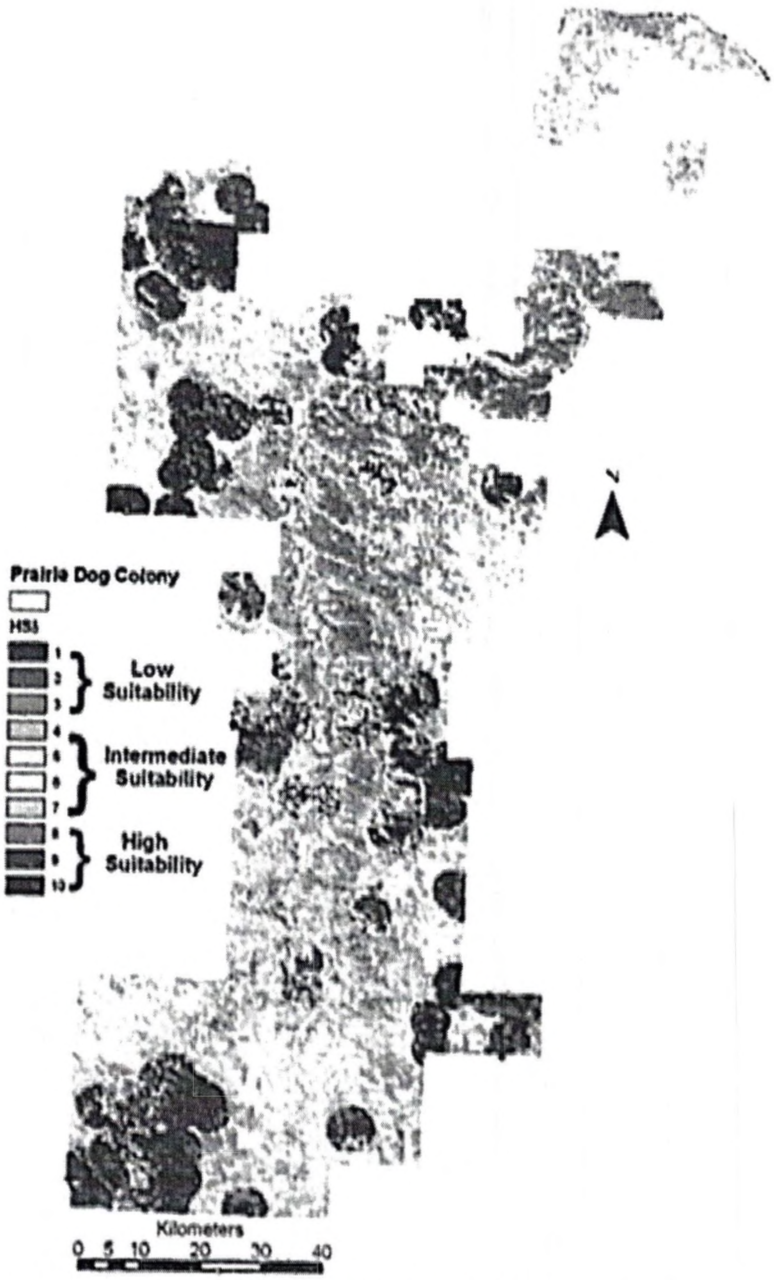


Figure 21. Output of the maximum dispersal distance habitat suitability model that integrated data on vegetation, slope, and maximum dispersal distance for characterizing the suitability of the Little Missouri National Grasslands for black-tailed prairie dogs. Habitat suitability index rankings were grouped into three classes (low, intermediate, high) for estimating the total areas by suitability class. Data on estimated areas of habitat within each suitability class are summarized in Table 9.

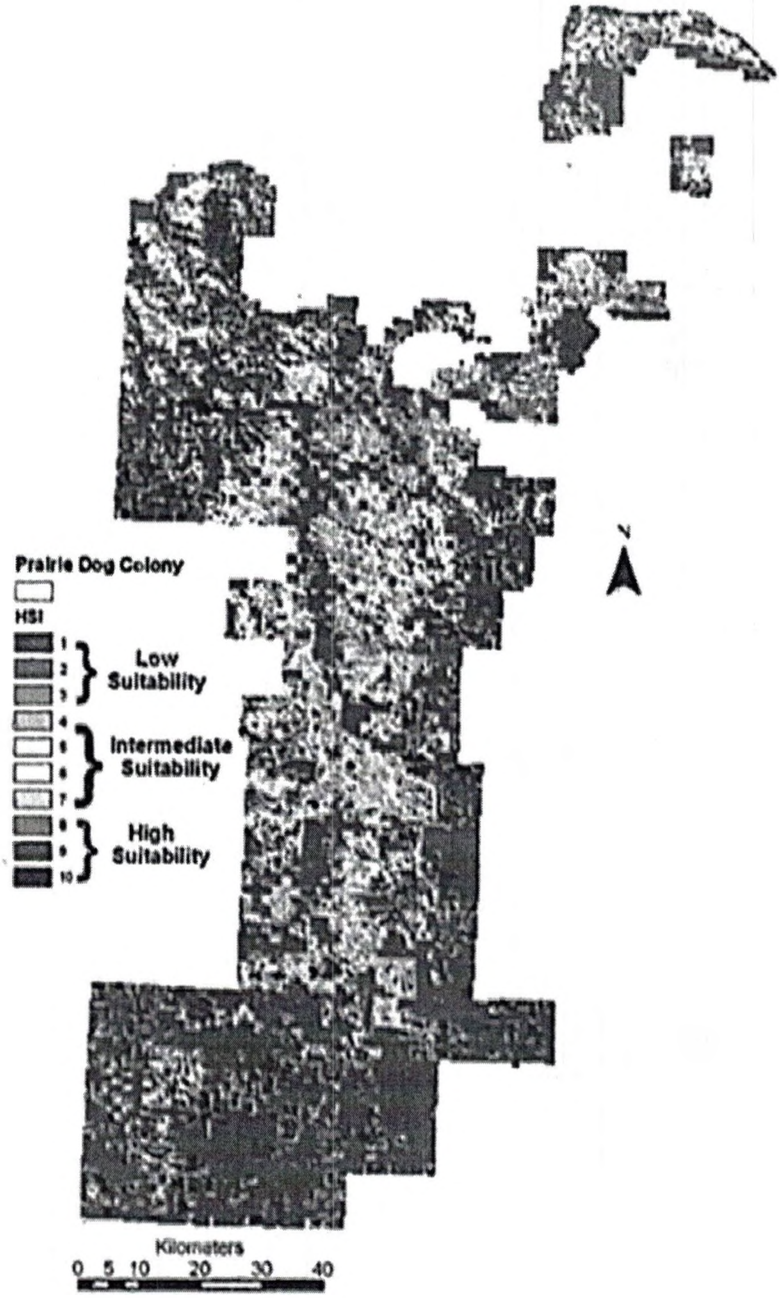
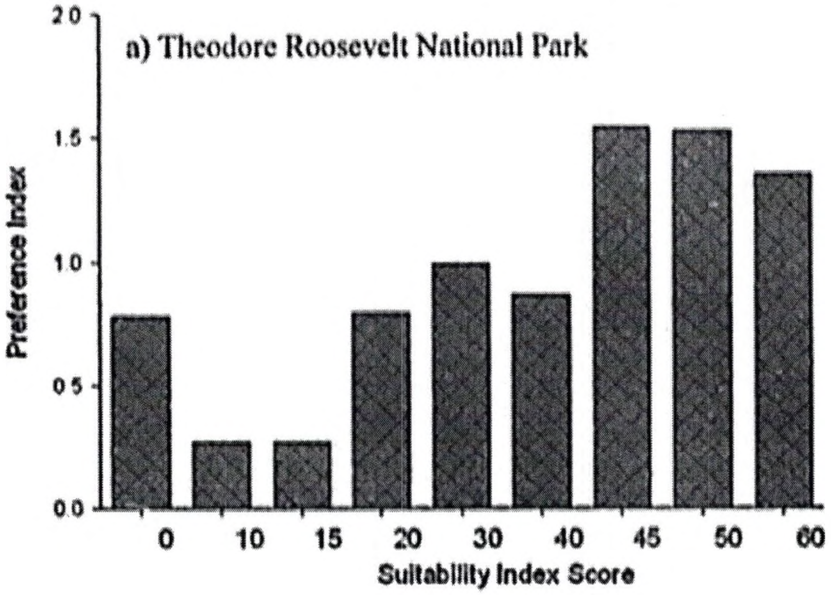


Figure 22. Output of the landownership habitat suitability model that integrated data on vegetation, slope, and landownership for characterizing the suitability of the Little Missouri National Grasslands for black-tailed prairie dogs. Habitat suitability index rankings were grouped into three classes (low, intermediate, high) for estimating the total areas by suitability class. Data on estimated areas of habitat within each suitability class are summarized in Table 9.

use high quality habitats with greater frequency than expected based upon availability, and analysis of habitat parameters indicated that habitat preference increased with increasing SI values. From this data set and my analysis, I conclude that prairie dogs selectively choose high quality habitats dominated by graminoids and slopes less than 5% and avoid areas dominated by trees and slopes greater than 25%. Prairie dog had an occupancy rate of 59% and 73% in habitats dominated by graminoids at Theodore Roosevelt National Park and in the Little Missouri National Grasslands, respectively (Figure 25), and a combined occupancy rate of 59% in habitats characterized by slopes ranging from 0-5% (Figure 26). When colonies were pooled, prairie dog colonies were found on average on slopes ranging from 4.8 to 5.3% slope based on 95% confidence intervals, suggesting an optimal slope of 5%. These results are in accordance with other efforts made to quantify the relationship between prairie dog presence and habitat characteristics. Reading and Matchett (1997) compared the occurrence of a variety of habitat characteristics on existing prairie dog colonies and randomly placed polygons in north central Montana using GIS and found that prairie dog colonies were located in habitats with an average slope of 5%. Reading and Matchett (1997) also reported that prairie dogs were more often found on state and federal lands than on private lands. More recently, Proctor (1998) developed and validated a HSI model using GIS and a classification tree approach for quantifying the relationship between prairie dog presence and habitat characteristics in north central Montana. Proctor's (1998) model indicated that prairie dogs used habitats characterized by low cover vegetation and slopes of 0 to 4%.



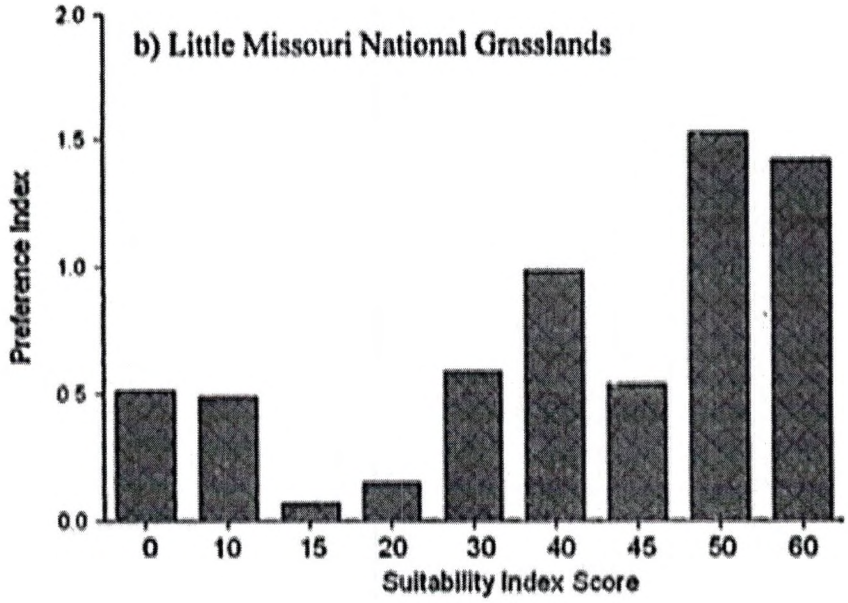


Figure 23. Plots of suitability index scores for the vegetation of colonies of black-tailed prairie dogs against estimated preference indices. Separate plots were produced for prairie dog colonies located at (a) Theodore Roosevelt National Park, and in the (b) Little Missouri National Grasslands, North Dakota. Preference indices were calculated using equation 2 (see text) and suitability index scores are defined in Table 7.

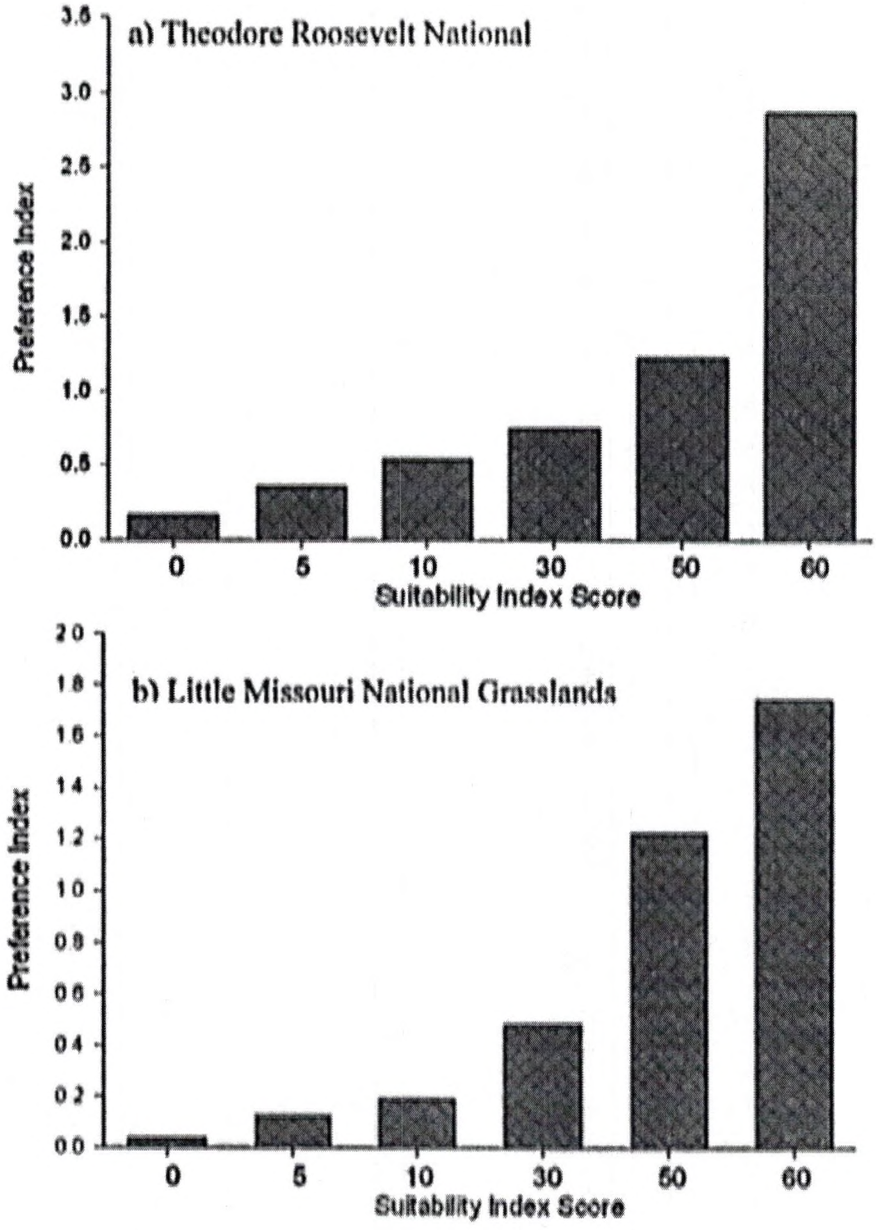


Figure 24. Plots of suitability index scores for the slopes of colonies of black-tailed prairie dogs against estimated preference indices. Separate plots were produced for prairie dog colonies located at (a) Theodore Roosevelt National Park, and in the (b) Little Missouri National Grasslands, North Dakota. Preference indices were calculated using equation 2 (see text) and suitability index scores are defined in Table 8.

Validation of the HSI models I developed suggests that they reliably predict areas of suitable prairie dog habitat. Nevertheless, proper application of these models requires an understanding of error and assumptions associated with model development. Although, a positive species-habitat relationship was found between high quality habitats as defined in the models, a greater than expected use of poor quality habitat was observed at Theodore Roosevelt National Park and the Little Missouri National Grasslands. Prairie dog presence in low quality habitats was usually observed at the colony peripheries where expansion pressures due to increased competition for food and mates caused prairie dogs to expand into sub-optimal habitats. Additionally, error associated with interpolation techniques and variation within pixel cells may have negatively biased preference for low quality habitats. At Theodore Roosevelt National Park, error associated with interpolation could not be quantified; however close examination of the data verified that some areas defined as HSI class 0 may not realistically characterize potential vegetation at a particular site. For example, at the Beef Corral Bottom prairie dog colony interpolation placed a large number of 0 valued pixels in the northwest corner of the colony where the edge of the colony is against a high butte. However, the colony itself is not located on the butte and it was unlikely that vegetation in the area of the colony was of the type found on buttes as predicted by interpolation. In the Little Missouri National Grasslands, greater than expected occupation of habitats dominated by badlands (HSI class 0) and agriculture (HSI class 10) may be attributed to problems with data resolution. Because pixel sizes were relatively large (30 m) important variation in vegetation characteristics within the cell may be lost or misrepresented. Additionally, the inability to tease out what type of agricultural practices were being implemented in habitats identified as agriculture could have affected the ability to accurately assess habitat quality in these areas.

Inherent in model development and validation are assumptions of prairie dog preference and use of habitat. Knowledge of these assumptions is critical for the proper interpretation and use of these models as a management tool. As stated earlier, there are three underlying assumptions for HSI modeling: 1) The study areas are within the range of the species of interest, 2) the species has unobstructed use of the habitat types used in the model, and 3) the population is not harvested in the area of interest. The first two assumptions for modeling were met because both study sites are located within the historic range of prairie dogs and prairie dogs have unobstructed use of their habitat. Conditions defined in assumption three were met at Theodore Roosevelt National Park but not in the Little Missouri National Grasslands. In the Little Missouri National Grasslands current management allows recreational shooting on both private and public lands, therefore models developed for the Little Missouri National Grasslands are in violation of assumption three. However, Mitchell et al. (2002) proposed a broader interpretation of assumption three, suggesting instead that the model should accurately reflect existing conditions for the population in which the model was tested. Under this more relaxed assumption models developed for the Little Missouri National Grasslands were justified. Because data used to formulate HSI classes came from both study sites and other areas within the historic range of prairie dogs under similar conditions, I suggest that the models developed for Theodore Roosevelt National Park and the Little Missouri National Grasslands were reasonable and unbiased.

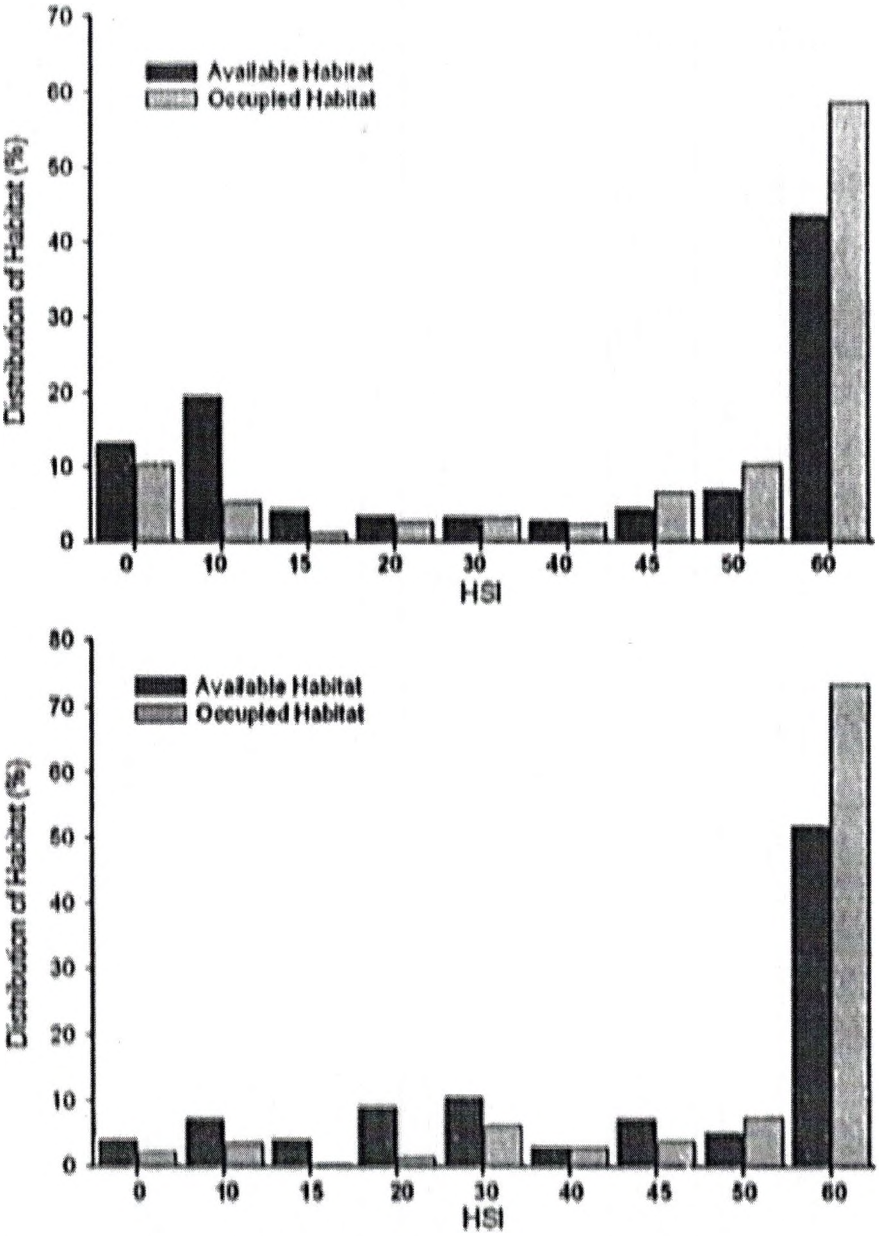


Figure 25. Plots of the estimated areas of available and occupied habitats of different suitability index scores for black-tailed prairie dogs at (a) Theodore Roosevelt National Park, and in (b) the Little Missouri National Grasslands. Information on the different habitat types found in each area and the associated suitability index scores for the habitat types are included in Table 7.

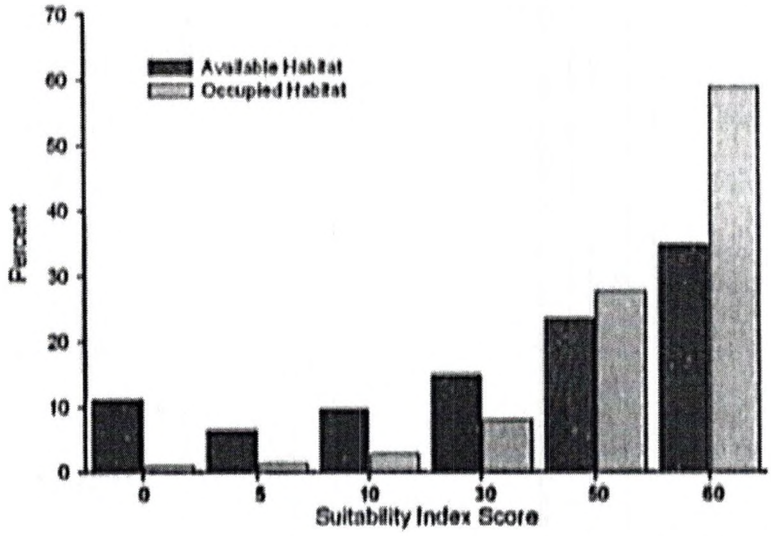


Figure 26. Plots of the estimated area of available and occupied habitat of different slope class and suitability index score for black-tailed prairie dogs at Theodore Roosevelt National Park and in the Little Missouri National Grasslands study areas. Information on the different slope categories and associated suitability index scores are included in Table 8.

Model error and assumptions associated with model development and validation discussed herein provide a foundation for understanding how HSI models can be used as a tool to manage wildlife. Understanding the implications of error and assumptions associated with model development will allow researchers and managers to determine how useful the model will be for each application. These models were developed on a relatively course scale and therefore should be applied to broad scale applications, such as identifying areas to investigate for potential prairie dogs reintroductions or management efforts. Although, these models are general; application of these models should be limited to areas within the region with similar topography and vegetation.

Conservation and Management Implications

In this paper I presented multiple models for both Theodore Roosevelt National Park and the Little Missouri National Grasslands, each with different definitions of habitat quality (SI scores) and management implications. The most basic models defined suitable habitat for prairie dogs based on vegetation, slope and landownership, whereas the effective and maximum dispersal models define potential prairie dog habitat based on the natural dispersal capabilities of prairie dogs. The basic habitat models are suitable for locating and quantifying the amount of suitable habitat available to prairie dogs, and for evaluating how changes in habitat management and landownership may influence or alter the availability of highly quality habitats. Information gained from these models may also be used for reestablishing colonies of prairie dog in areas that are unlikely to be naturally colonized. The effective dispersal model identifies areas and habitats that may be naturally colonized by prairie dogs in the near future. The maximum dispersal model also identifies areas with a high probability of natural colonization, but over a somewhat longer term. The ability to identify areas within the dispersal capabilities of prairie dogs and likely to support prairie dogs through natural colonization will help mangers focus prairie dog recovery efforts in areas where habitat manipulations or reintroductions may be necessary for the recovery of prairie dog population. Information derived from these models will provide biologists and researchers with a mechanism for making meaningful decisions based on scientific knowledge regarding the future management of prairie dogs and their associated species.

CHAPTER 4

RELATIVE ABUNDANCE AND ASPECTS OF THE DISTRIBUTION OF BLACK-TAILED PRAIRIE DOGS IN WESTERN NORTH DAKOTA

" The village of those animals covers about 4 acres... and contains great numbers of holes on the tope of which those little animals sit erect and make a whistling noise and when alarmed slip into their hole... "

--- Lewis and Clark, 1804

Introduction

Black-tailed prairie dogs (*Cynomys ludovicianus*) are small, colonial rodents that were historically widespread in North America's short and mixed-grass prairies. Although there has been recent debate regarding the level of the species' historical abundance (Knowles et al. 2002, Virchow and Hygnstrom 2002), there is no doubt that the combination of poisoning, agricultural development and disease have decimated the species in recent years (Barnes 1993, Van Pelt 1999, Forest 2002). In prairie ecosystems the black-tailed dog is considered a keystone species whose presence and activities support a diversity of vertebrates and invertebrate species (Stapp 1998, Kotliar et al. 1999, Lomolino and Smith 2003). Because of the importance of prairie dogs for the diversity and overall function of grassland ecosystems, considerable interest is now focused on managing the species to promote long-term population persistence (American Society of Mammalogists 1998, Van Pelt 1999, Sidle et al. 2001, Johnson and Collinge 2004).

In North Dakota, the historic range of black-tailed prairie dogs encompassed most of the southwestern portion of the state (Sidle et al. 2001, Knowles 2002). Similar to the pattern for other parts of North America, the numbers and area occupied by colonies of black-tailed prairie dogs declined from the late 1800s to approximately the mid 1980s (Bishop and Culbertson 1976). Beginning in the late 1800s and continuing through the mid 1960s, prairie dogs were substantially reduced in number by settlers, the U.S. Bureau of Biological Survey and North Dakota Department of Agriculture. For example, between 1915 and 1964 the North Dakota Department of Agriculture initiated a poisoning campaign covering over 209,400 ha of prairie dog colony area (Bell 1921, Forrest 2002), and by 1961 the statewide colony acreage for the species had been reduced to an estimated 7,991 ha (Van Pelt 1999). Also, Bishop and Culbertson (1976) used photographs and other records to document an approximate 89% reduction in the number of prairie dog colonies within the Medora Ranger District of the Little Missouri National Grasslands between 1938 and 1972.

Changes in management activities on federal and state lands and bans on some poisons in the 1970s helped prevent wholesale eradication of black-tailed prairie dogs in North Dakota. Even with these changes, however, the subsequent recovery of prairie dogs in North Dakota has been slow. By the 1980s there was an estimated statewide prairie dog colony acreage of 8,092 ha (Van Pelt 1999), and in 2002 Knowles (2003) reported a minimum estimate of 8,122 ha of prairie dog colonies occurring between two population centers in the state, the Little Missouri Complex and the Standing Rock Complex (Figure 27). The Little Missouri Complex is located in the far southwestern portion of North Dakota including the Little Missouri National Grasslands, the north and south units of Theodore Roosevelt National Park, and other private and state lands in McKenzie, Billings, Golden Valley, and Slope Counties (Figure 27). The Standing Rock Complex is located in the south-central portion of North Dakota including the Standing Rock Sioux Indian Reservation and adjacent lands in Grant and Morton counties (Knowles 2003; Figure 27).

An estimated 2,862 ha or 35% of the current range of black-tailed prairie dogs in North Dakota is within the geographical boundaries of the Little Missouri National Grasslands and the North and South Units of Theodore Roosevelt National Park. The revised USDA Forest Service management plan for the Little Missouri National Grasslands identifies as a key objective the long-term maintenance of plant and animal species diversity and ecosystem function, and includes specific provisions and goals for increasing the abundance and colony acreages of black-tailed prairie dogs. As part of the management plan for prairie dogs in the Little Missouri National Grasslands, colony boundaries and acreages have been periodically evaluated or re-mapped every 5-6 years since 1997. Theodore Roosevelt National Park is managed for the long-term preservation of cultural and natural resources and minimal human interference in population processes for species like the black-tailed prairie dog (Resource Management Plan, TRNP 1994). Prairie dog colonies have been regularly mapped in the north and south units of the park since 1947, and in recent years the areas and margins of all colonies have been updated every 2 to 3 years.

Because of concern over the long-term viability of black-tailed prairie dogs across their distributional range including in North Dakota, quantitative estimates of populations are needed for monitoring the status of the species. Three methods have been used for

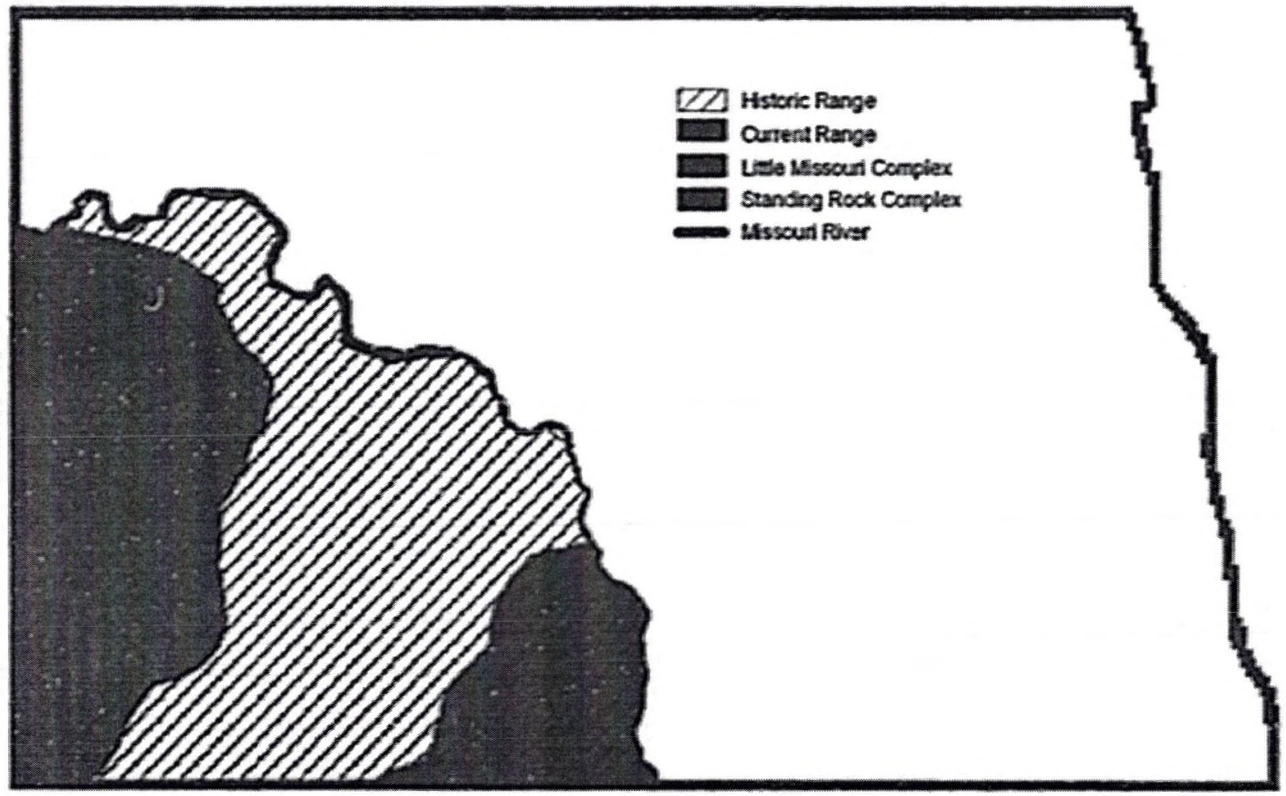


Figure 27. Map showing the historic and current range of black-tailed prairie dogs in North Dakota. The current range is composed of two population centers: the Little Missouri Complex and the Standing Rock Complex and is based on the locations of prairie dog colonies mapped in 2002 by Knowles (2003).

estimating prairie dog abundance and density; counts of active burrows (Tietjen and Matschke 1982, Biggins et al. 1993), mark-recapture (Otis et al. 1978, Seber 1982, Menkens and Anderson 1989), and visual counts (Fagerstone and Biggins 1986, Knowles 1986, Powell et al. 1994). Empirical research suggests that counts of active burrows may not be especially reliable for estimating prairie dog populations (Knowles 1982, Menkens et al. 1988, Powell et al. 1994, but see Johnson and Collinge 2004). Mark-recapture methods are useful for estimating prairie dog numbers (Menkens et al. 1988) but the technique is not cost effective for widespread and regular use for species like prairie dogs that occur in multiple isolated or semi-isolated populations over large areas (Menkens et al. 1990). Several studies have demonstrated that prairie dog population estimates from visual count surveys are well correlated with population estimates based on mark-recapture (Fagerstone and Biggins 1986, Severson and Plumb 1998). Visual count surveys can be repeated at multiple prairie dog colonies over a relatively short time frame (Fagerstone and Biggins 1986, Johnson and Collinge 2004) and may therefore provide a means for rapidly assessing the population density of many individual colonies when data on colony areas are also available. My primary objective in this study was to use visual counts at multiple individual colonies in the Little Missouri National Grasslands and Theodore Roosevelt National Park to estimate mean prairie dog densities and the overall population size in the region from data on colony area. I also evaluated a suite of different variables potentially contributing to variation in individual colony densities.

Study Area

The Little Missouri National Grasslands is located along the Little Missouri River corridor, an area characterized by flat plateaus, rugged canyons, and alluvial benches associated with the Little Missouri River and its tributaries. The Little Missouri National Grasslands are divided into two districts, the Medora Ranger District in the south and the McKenzie Ranger District in the north, together encompassing 415,929 ha of intermingled federal, state and private land. Theodore Roosevelt National Park is composed of three units, the North Unit (9,738 ha), South Unit (18,663 ha) and the Elkhorn Ranch Unit (88 ha), all located entirely within the Little Missouri National Grasslands. A total of 189 prairie dog colonies are located in the Little Missouri National Grasslands (119 in the Medora Ranger District and 70 in the McKenzie Ranger District; Knowles 2003), whereas the North and South Units of Theodore Roosevelt National Park harbor 20 and three prairie dog colonies, respectively. The Elkhorn Ranch Unit of Theodore Roosevelt National Park does not encompass any prairie dog colonies. Prairie dog colony acreages are estimated at 2,364 ha for the Little Missouri National Grasslands (1,656 ha in the Medora Ranger District and 708 ha in the McKenzie Ranger District) and 498 ha for Theodore Roosevelt National Park (59 ha in the North Unit and 439 ha in the South Unit).

Management of black-tailed prairie dogs at Theodore Roosevelt National Park and the Little Missouri National Grasslands differs in ways that may promote variable population dynamics or density between areas. Prairie dogs at Theodore Roosevelt National Park have been protected from poisoning and shooting since the late 1940s and minimal or no active efforts are used to limit population growth. Prairie dogs in the Little Missouri National Grasslands are the focus of an active recreational hunting program in both the Medora and McKenzie Ranger districts. Also, prairie dogs in the grasslands region may be controlled by a limited range of poisons but only when colonies impinge on adjacent private lands (poisoning is legal on private lands in the area).

Vegetation in the region encompassing the Little Missouri National Grasslands and Theodore Roosevelt National Park is dominated by western wheatgrass (*Agropyron smithii*), blue grama (*Bouteloua gracilis*), little bluestem (*Schizachyrium scoparium*) and silver sagebrush (*Artemisia cana*) on the rolling hills and prairies, rocky mountain juniper (*Juniperus scopularum*) and green ash (*Fraxinus pennsylvanica*) along the woody draws, and eastern cottonwood (*Populus deltoides*) along the river. Soils belong to the Bainville Series, developed from excessively drained medium-texture, calcareous parent material. Elevation ranges from 550 to 1,070 m throughout the study sites. The climate is characterized as semi-arid with long cold winters and short hot summers; temperatures range from an average low of −11.6 °C in January to an average high of 22 °C in July. Average annual rainfall is 380 mm, with most precipitation falling in early summer (May and June).

Methods

Developing representative estimates of prairie dog density for estimating population size required random subsampling of individual colonies for visual count surveys. Preliminary study design analyses indicated that visual counts on approximately 30 randomly selected prairie dog colonies within the Little Missouri National Grasslands would be sufficient for reliably estimating the regional density. Based on the proportional areas of each district, I targeted 10 colonies for visual counts in the McKenzie Ranger District and 20 colonies for visual counts in the Medora Ranger

District (Figure 28, 29). As another part of the colony selection procedure I identified all colonies on public lands that were larger than 8 ha (minimum size required for a visual count-based density estimate; Severson and Plumb 1998) and divided them into three size classes: small (8-15 ha), medium (16-34 ha), and large (35-120 ha). In the McKenzie Ranger District I randomly identified five 8-15 ha colonies, three 16-34 ha colonies and two 35-120 ha colonies for study. In the Medora Ranger District I randomly identified six 8-15 ha colonies, eight 16-34 ha colonies and six 35-120 ha colonies for study. A total of five prairie dog colonies were used to estimate a visual count-based density for Theodore Roosevelt National Park (Figure 29). At Theodore Roosevelt National Park there were 16 total colonies larger than 8 ha (14 in the South Unit and two in the North Unit) for possible selection. Visual count surveys were restricted to colonies in the South Unit of the park, however, because of ongoing research at three colonies in the area. Five total colonies in the South Unit were used for the visual count density estimate for Theodore Roosevelt National Park including three colonies in the 35-120 ha size range and two colonies in the 16-34 ha size range. Randomization procedures were not used to identify the five colonies for visual count research at Theodore Roosevelt National Park, instead they were constrained to include the three colonies being used as part of a related study (see Chapter 2), and two colonies that were readily accessible for the vehicle-mounted observation platform (off road vehicle use is prohibited in the National Park System).

All visual count surveys were conducted in the summer period between June 15 and August 15 when the rate of change in prairie dog populations appears minimal (Hoogland 1995, Severson and Plumb 1998). Visual counts were focused in the morning

Figure 28. Distribution of prairie dog colonies in the McKenzie Ranger District in 2002. Colonies highlighted in red were randomly selected for surveyed to estimate colony density.

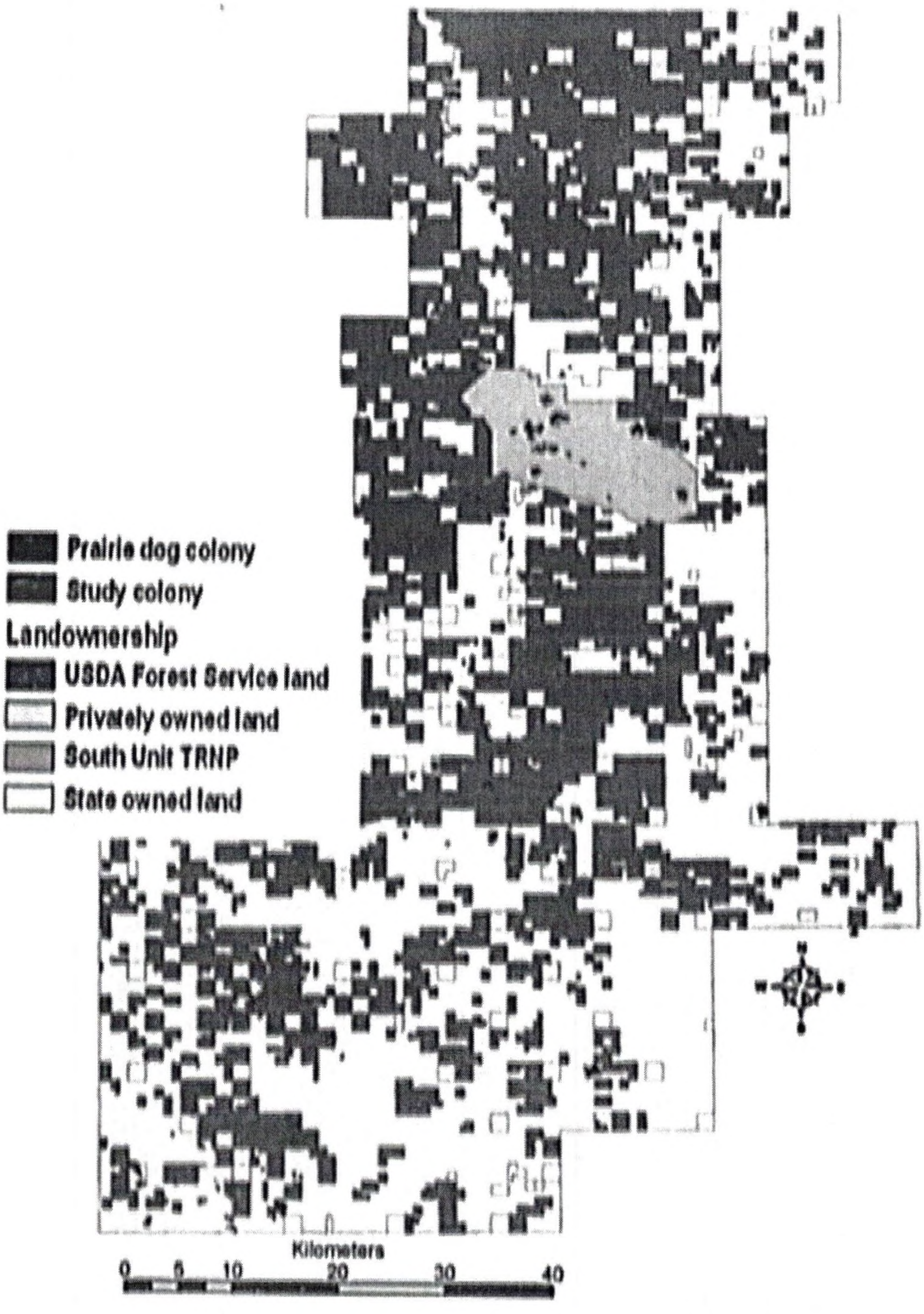


Figure 29. Distribution of prairie dog colonies in the Medora Ranger District in 2002 and Theodore Roosevelt National Park in 2003. Colonies highlighted in red were randomly selected for to estimate colony density.

(0730 to 1100 hrs) and evening (1800 to 2100 hrs) periods when prairie dogs are relatively active aboveground (Hoogland 1995). Colonies were representatively sampled by marking out two different 2 to 4 ha plots on each colony where two different technicians stationed on elevated observation platforms conducted independent timed visual counts (Severson and Plumb 1998). Visual counts were done from a 1.5-m observation platform mounted in the bed of a pick-up truck (Little Missouri National Grasslands and two colonies at Theodore Roosevelt National Park) or from 4-m observation towers (three colonies at Theodore Roosevelt National Park). The vehicle-mounted observation platform was parked a minimum of one hour prior to the first visual count in an elevated location allowing unobstructed views of both sampling plots. Based on the recommended visual count protocol, six consecutive counts at 20-minute intervals were conducted by each observer on each of three different days within a 7 to10 day time period. Visual counts were equally divided between morning and evening time sessions, where each colony was the focus of three days of morning counts or three days of evening counts. During each 20-minute visual count period both technicians systematically scanned each plot once and recorded the maximum number of prairie dogs observed. The highest maximum count noted by an individual observer for each 20-minute count was used to estimate the density for a colony (Severson and Plumb 1998). Prior to initiating a visual count I noted and recorded weather conditions using a Kestrel 3000 weather system (Nielsen-Kellerman, Boothwyn, PA). Because strong winds (> 32 km/h) and inclement weather (rain, wind speeds > 32 km/h) can restrict aboveground activity of prairie dogs, visual counts were limited to periods with no precipitation, wind speed < 32 km/h, and ambient temperatures > 10 °C. Shooting by recreational hunters also depresses aboveground activity by live prairie dogs. If recreational hunters were present or arrived during a visual count, counts were postponed and resumed within one day as conditions allowed.

Population Estimates from Colony Densities

Data from visual count surveys were used to estimate the population density at each sampled colony based on the protocol and equations recommended by Severson and Plumb (1998). Severson and Plumb (1998) provided an equation for estimating prairie dog density/ha (P) as:

$$P = ([Y/S_p] - 3.04)/0.04$$

where Y is the maximum count of prairie dogs in a replicate for each colony and S_p is the total area sampled. Density calculations were then adjusted for the probability of not observing all prairie dogs during a count using an adjustment coefficient based on mark-recapture data (Severson and Plumb 1998). Separate mean colony densities were calculated from visual count data for the Medora Ranger District, the McKenzie Ranger District, and Theodore Roosevelt National Park. A one-way analysis of variance revealed variation in mean colony density among the three areas ($F_{2\text{-}21} = 4.59$, $P = 0.022$). I therefore used the separate densities for each area to calculate population estimates based on the equation:

$$T = S_c \times P$$

where S_c is the total colony size in hectares and P is the estimated density per hectare for the park unit or ranger district as appropriate. Sizes of individual prairie dog colonies in hectares were converted from acreages reported by Knowles (2003) for colonies located within the Little Missouri National Grasslands in 2002, and from colony acreages for

Theodore Roosevelt National Park based on surveys in summer 2003. The sum of estimated populations for all individual prairie dog colonies was used to provide an estimate of the overall population of prairie dogs in the McKenzie and Medora Ranger Districts of the Little Missouri National Grasslands.

Variables Influencing Black-tailed Prairie Dog Density

Prairie dog density may be influenced by a variety of biotic and abiotic factors several of which are at least partly related to management. I used habitat features and other data to evaluate several parameters potentially contributing to regional variation in prairie dog densities in the study area region. Black-tailed prairie dogs are a highly social and colonial species (Hoogland 1995) and colony density may therefore be influenced by the presence of conspecifics in neighboring colonies. Proximity to roads has been shown to influence the abundance and distribution of a variety of wildlife species, often related to increased human access to natural areas (Mladenoff et al. 1995). In western North Dakota a network of roads and trails provides vehicle access to prairie dog colonies for recreational shooting and may also be used as a means for dispersal (Knowles 1985), which may have the effect of depressing population density. I used a geographic information system (GIS; ArcView 3.2, ESRI, Redlands, CA) to calculate distances from study colonies to the nearest adjacent colonies, and distances from study colonies to nearest roads. Distances were based on shortest straight-line distance between the centroids of each study colony to the nearest neighboring colony or the nearest road determined by the Nearest Neighbor Extension for ArcView 3.2 (Weigel 1992). In addition, I evaluated the potential effect colony size may have on individual colony density. Data on colony acreage were obtained from Knowles (2002) for the Little

Missouri National Grasslands and from park records at Theodore Roosevelt National Park (TRNP records). A series of linear regression models were estimated to evaluate the potential effects of distance to roads, proximity to nearby colonies, and overall colony size on estimated colony densities.

Results

I was able to complete visual count surveys on 19 prairie dog colonies located within the McKenzie and Medora Ranger Districts of the Little Missouri National Grasslands, and five prairie dog colonies in the South Unit of Theodore Roosevelt National Park during summer 2003 (Figures 28, 29). Although I had identified and targeted 30 randomly selected colonies for visual counts, the combination of inclement weather, disturbances by recreational shooters, and inaccessibility of several prairie dog colonies limited the research effort. Of the original 30 colonies selected and targeted for study in the Little Missouri National Grasslands, nine were either inaccessible by damaged roads or otherwise poorly suited for sampling, one had limited visibility by a large livestock water holding tank and corral, four colonies were not adequately sampled with the requisite numbers of timed counts because of weather or disturbance by recreational hunters, and time and other logistical constraints precluded visual counts at five colonies near the end of the summer study period.

Visual count data suggested significant variation in densities for individual colonies and among the three broadly defined areas of the study region (Table 10). The highest estimated density was 108.0 prairie dogs/ha for a colony in the McKenzie Ranger District whereas the lowest estimated density was 7.4 prairie dogs/ha for a colony in the Medora Ranger District (Table 10). Statistical comparisons indicated that mean colony densities were different among the Medora and McKenzie Ranger Districts and Theodore Roosevelt National Park ($F_{2,21} = 4.59$, $P = 0.022$; Table 10). Post hoc pairwise comparisons suggested lower prairie dog colony densities for the Medora District compared to the McKenzie district in 2003 (Bonferroni corrected $P = 0.019$; Table 10), but mean colony densities were similar for Theodore Roosevelt National Park and the Medora District, and for the park and the McKenzie District (Bonferroni corrected P values ≥ 0.50; Table 10).

I summarized data on the total areas for the 189 prairie dog colonies located within the Little Missouri National Grasslands and for the 23 prairie dog colonies at Theodore Roosevelt National for calculating population estimates from mean densities (Table 11). Based on estimated colony acreages for the Little Missouri National Grasslands from 2002 and estimated colony densities from the area in summer 2003, I estimated there were 42,791 and 46,725 black-tailed prairie dogs in the McKenzie and Medora Ranger Districts, respectively (Table 11). Data on colony areas and mean colony density suggested there were 18,530 and 2,482 prairie dogs in the South and North Units of Theodore Roosevelt National Park, respectively (Table 11). For the entire study region there were approximately 110,528 prairie dogs in summer 2003 (Table 11).

Although there was variation in the density of individual prairie dog colonies (Table 10), colony density was not closely linked to colony size ($r^2 = 0.001$, $P = 0.876$), distance to roads ($r^2 = 0.036$, $P = 0.374$), or distance to the nearest occupied prairie dog colony ($r^2 = 0.011$, $P = 0.636$; Figure 30, Table 12).

Table 10. Estimated prairie dog colony densities in summer 2003 for the McKenzie and Medora Ranger Districts in the Little Missouri National Grasslands, and in the South Unit of Theodore Roosevelt National Park.

McKenzie Ranger District		Medora Ranger District		Theodore Roosevelt National Park	
Prairie dog colony	Density (pd/ha)	Prairie dog colony	Density (pd/ha)	Prairie dog colony	Density (pd/ha)
14	29.9	91	7.4	PV[1]	20.7
11	31.8	125	9.9	JP	31.8
65	36.2	101	13.7	HW	35.3
42	42.4	81	23.4	BC	35.7
52	74.5	99	28	MA	87.4
27	79.9	168	31.2		
18	80.7	144	33		
49	108	164	42.4		
		171	42.4		
		159	43		
		146	43.7		
Average ± SE	0.4 ±10.3	Average ± SE	28.9 ± 4.1	Average ± SE	42.2 ± 11.6

[1] PV = Peaceful Valley, JP = Johnson's Plateau, HW = Halliday Well, BC = Beef Corral Bottom, MA = Mike Auney prairie dogs colonies

Table 11. Data on estimated abundance or populations of black-tailed prairie dogs in the Little Missouri National Grasslands, Theodore Roosevelt National Park, and the entire Little Missouri National Grasslands region. Data and estimates are based on research conducted in summer 2003.

Area	Total # of colonies	Estimated colony area (ha)	Average density pd/ha	Estimated abundance	95% lower limit [a]	95% upper limit [b]
Theodore Roosevelt National Park						
South Unit	20	439	42.2	18,530	7,113	29,946
North Unit	3	59	42.2[c]	2,482	953	4,011
Little Missouri National Grasslands						
McKenzie Ranger District	70	708	60.4	42,791	28,480	57,101
Medora Ranger District	119	1,656	28.9	46,725	33,540	59,910
Estimated overall population	212	2,862		110,527	70,086	150,968

[a] Lower value for the 95% confidence interval for mean abundance
[b] Upper value for the 95% confidence interval for mean abundance
[c] Based on the mean density for the South Unit of Theodore Roosevelt National Park

Discussion

Black-tailed prairie dogs are widely distributed in both the McKenzie and Medora Ranger Districts of the Little Missouri National Grasslands and at Theodore Roosevelt National Park (Figures 28, 29). Results from this research revealed considerable variation in colony density among the 24 study colonies in the Little Missouri National Grasslands and at Theodore Roosevelt National Park (Figure 31). Nevertheless, The estimated prairie dog were within the range of colony densities for black-tailed prairie dogs in multiple National Parks or National Monuments elsewhere in the United States (Plumb and Willison 1995). Interestingly, however, my research suggested relatively low colony densities in the Medora Ranger District of the grasslands (Figure 31; Table 10), which may or may not indicate a potential management problem. Additional count surveys should be conducted in the Medora Ranger District area to get a better idea of how representative my 2003 sample counts were for colonies in this region.

I was unable to explain the variation in colony density observed by proximity to the nearest occupied prairie dog colony, proximity to roads, or colony size. One factor that I was unable to directly evaluate that may be important for colony density is predation pressure. Anecdotal evidence from research at Theodore Roosevelt National Park suggests that the presence of predators can dramatically reduce prairie dog numbers over a short period of time. Prairie dog activity in one study of my multiple year study colony at Theodore Roosevelt National Park was reduced when a family of badgers (*Taxidea taxus*) became established in the area in spring and summer 2003 (also discussed in Chapter 2). When I was conducting visual count surveys at individual study colonies I recorded data on observations of different mammalian predators (badger;

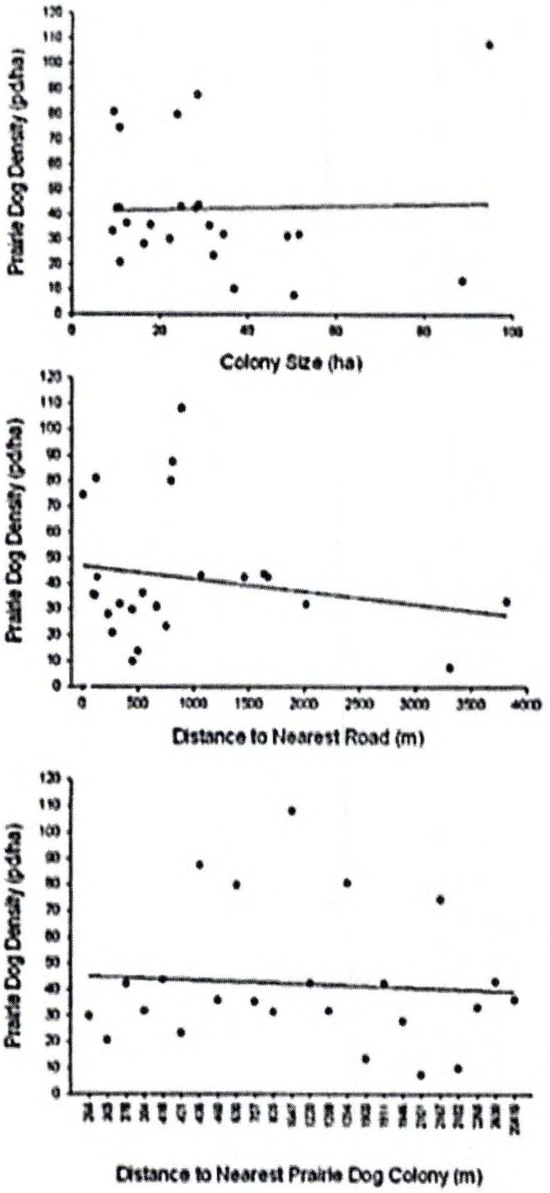


Figure 30. Estimated prairie dog densities for different colonies evaluated by (a) colony size (b) distance to nearest road, and (c) distance to nearest prairie dog colony for prairie dog colonies in the Little Missouri National Grasslands and Theodore Roosevelt National Park.

Table 12. Attributes associated with sampled prairie dog colonies in the McKenzie (MKRD) and Medora (MRD) Ranger Districts in the Little Missouri National Grasslands and in the South Unit of Theodore Roosevelt National Park (TRNP).

Area	Prairie dog colony	Density (pd/ha)	Colony size (ha)	Minimum distance to nearest road (m)	Minimum distance to nearest pd colony (m)
MKRD	14	29.9	22.1	450	264
MKRD	11	31.8	51.7	2,022	1,288
MKRD	65	36.2	12.5	541	20,410
MKRD	42	42.4	10.7	132	1,911
MKRD	52	74.5	10.8	5	2,167
MKRD	27	79.9	23.9	792	630
MKRD	18	80.7	9.5	122	1,394
MKRD	49	108	94.6	888	1,047
MRD	91	7.4	50.5	3,310	2,102
MRD	125	9.9	37	451	2,182
MRD	101	13.6	88.6	501	1,900
MRD	81	23.4	32.2	754	421
MRD	99	28	16.4	235	1,946
MRD	168	31.2	49.1	667	825
MRD	144	33	9.3	3,819	2,265
MRD	164	42.4	10.2	1,673	378
MRD	171	42.4	28.1	1,460	1,221
MRD	159	43	24.8	1,068	2,630
MRD	146	43.7	28.9	1,637	418
TRNP	PV[1]	20.7	11	269	366
TRNP	JP	31.8	34.5	2,022	1,288
TRNP	HW	35.3	31.4	113	757
TRNP	BC	35.7	17.8	95	384
TRNP	MA	87.4	28.9	811	436

[1] PV = Peaceful Valley, JP = Johnson's Plateau, HW = Halliday Well, BC = Beef Corral Bottom, and MA = Mike Auney prairie dog colonies

coyote, *Canis latrans*) and raptors (golden eagle, *Aquila chrysaetos;* ferruginous hawk, *Buteo regalis;* northern harrier, *Circus cyaneus*; burrowing owl). Mammalian predators were observed on 29% of the sampled colonies, whereas raptors were noted on 33% of the sampled colonies. However, because I spent a relatively brief time at each colony, I did not consider that I had sufficient quantitative data on predation and predation pressure to assess the importance of this factor on observed colony densities.

This study was not designed to quantify the level of hunting pressure at each colony, but several lines of evidence suggest hunting was not a key limiting factor in summer 2003. First, hunters typically access prairie dog colonies by road, and the lack a significant association between proximity to roads and colony density, indirectly suggested that shooting may not limit prairie dog colony density in the Little Missouri National Grasslands. Reading and Matchett (1997) were also unable to link road density to prairie dog abundance. Secondly, my estimated mean colony density was higher for the Medora Ranger District of the grasslands compared to Theodore Roosevelt National Park, where poisoning and shooting is illegal. Third, over the course of the study I directly observed recreational hunters at 47% of the study colonies and indirect evidence of hunting was present at all of them. Thus, although recreational hunting of prairie dogs is popular and common in the Little Missouri National Grasslands, more detailed research will be needed to evaluate the importance of this activity on prairie dog populations in North Dakota.

The continuation of long-term monitoring of prairie dog abundance and distribution in the Little Missouri National Grasslands region will be important for effective management of the species in western North Dakota. These types of data are valuable for converting data on acreages into estimates of population size. The results from this study will provide a baseline of information for comparison to similar data from other areas including other national grasslands in other states. For North Dakota in particular, this type of baseline information will be valuable for detecting any potential long-term changes in prairie dog abundance as different management approaches are applied as part of efforts to conserve and recover populations.

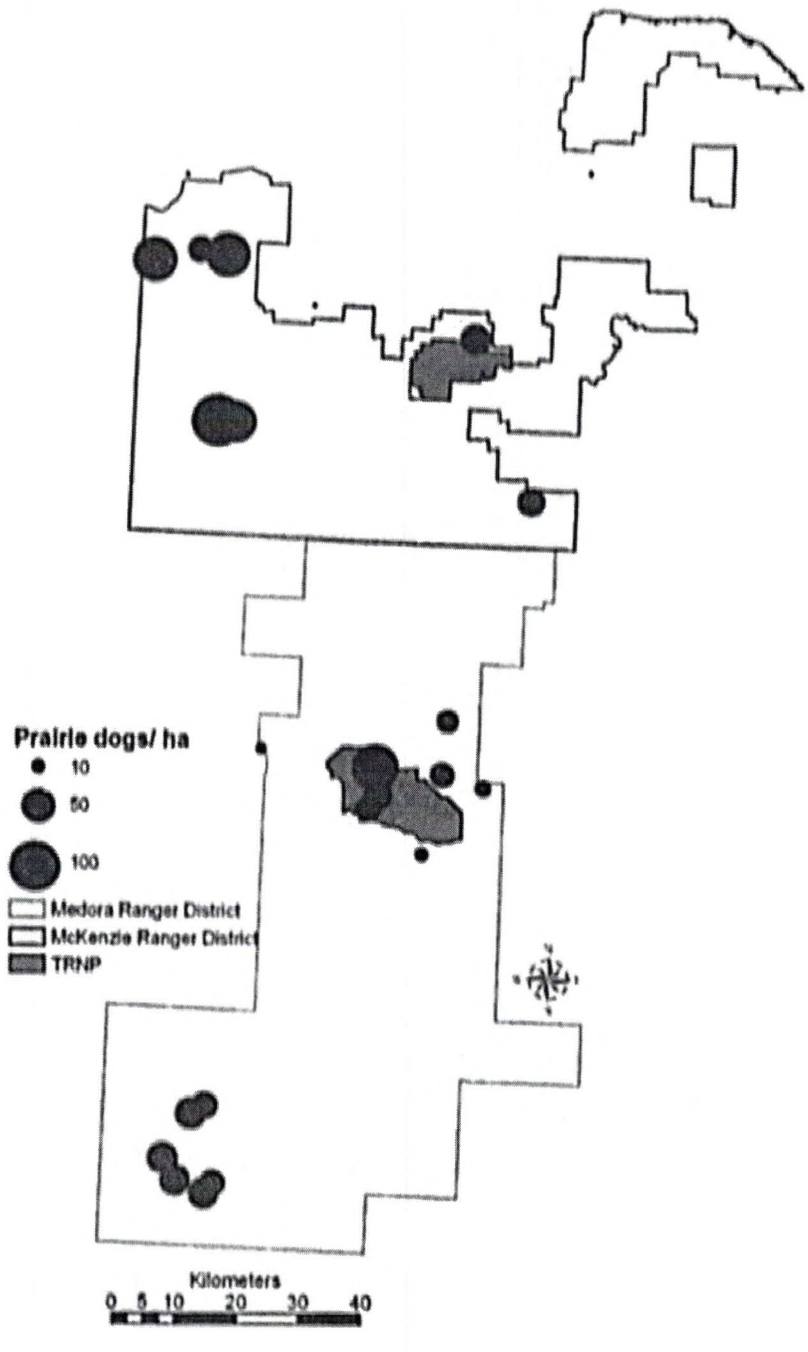


Figure 31. Estimated prairie dog densities for selected prairie dog colonies in the Little Missouri National Grasslands and at Theodore Roosevelt National Park in 2003. Prairie dog densities ranged from 7 to 108 prairie dogs/ha.

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